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RESPONSES OF CAPTIVE ALLIGATORS TO AUDITORY STIMULATION¹

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INTRODUCTION

THREE types of vocalization have been described for the American alligator (*Alligator mississippiensis*) and speculations have been offered as to the significance of each call. A series of short grunts, "umph! umph! umph!" may be given by the animals from birth to maturity according to McIlhenny (1935) who recorded the emission of this sound by a male which was attacked by another of its species. A sharp "hiss" occurs frequently when the alligator is "disturbed" (Berridge, 1926) or "angry" (McIlhenny, 1935); and the hiss may be combined with the roar when one adult male is "seeking encounter" with another (McIlhenny, 1935).

The bellowing or roaring of the full-grown alligator has been described by many observers. In the South-eastern United States this reptile breeds during early summer, and it is at this time that roaring is most frequently heard (True, 1893; Reese, 1907; Harper, 1930; McIlhenny, 1935). Roaring continues with diminishing frequency throughout the warm summer months and is rare during the winter (Harper, 1930; McIlhenny, 1935). We have been unable to find any published accounts of observed matings in *Alligator mississippiensis*, but according to Descourtilz (1809) a closely related species ("Cai-

¹ Contribution from the Department of Animal Behavior, The American Museum of Natural History, New York, N. Y.

man'') roars during copulation; and Wosseler (1915), who observed the courtship of Nile crocodiles (*Crocodylus niloticus*) in the Hamburg Zoological Gardens, reports that similar vocalization occurs in this species.

Although the point is not conclusively established it is probable that the roar is emitted only by the male alligator. Similarly, in the crocodile (*C. niloticus*) it is apparently only the male that roars (Schmidt, 1919). The function of the call has been variously interpreted. Harper (1930) suggests that it may serve as a mating call during breeding season, but this is obviously not an exclusive function, since the roar also occurs at other times of the year. McIlhenny (1935) believes that the male's roar is a challenge to other breeding males and holds no attraction for the female of the species. In the course of field observations both Harper and McIlhenny found that the roaring of one male is very likely to stimulate similar vocalization on the part of others in the vicinity; in fact, McIlhenny states that if other adult males are within hearing they are certain to answer.

The roar has been described by different authors as a "loud, deep-toned booming sound" (Berridge, 1926), and as "something like [the cry of] a bull frog, but intensified like distant thunder" (True, 1893). According to McIlhenny (1935) there is "no sound natural or artificial which causes such a tremendous vibration of the atmosphere." Ditmars (1910) states that although 5-foot males can roar, the sound produced by a 10- to 12-foot specimen is very much louder. The roar of an adult bull is said to be audible for at least three miles. The Caiman's "angry roar" (Descourtilz, 1809) and the Nile crocodile's "gasping roar" (Wosseler, 1915) are apparently quite similar to the vocalization of the American alligator.

The position and behavior of the alligator at the time of roaring has been observed by Harper (1930) and by McIlhenny (1935) whose accounts agree in all essential details. Roaring occurs most frequently when the alli-

gator is swimming or floating in the water. Occasionally an animal may roar when it is half in the water and half on the bank; but McIlhenny states that this call is never given when the reptile's body is entirely on land. When the alligator roars while in the water the head is thrown upward at a sharp angle to the back and points out of the water at an angle of 30 to 40 degrees. The tail is raised in an arc above the water and the tip bends downward to touch the surface. The tail is moved from side to side and the alligator thus "sculls" himself along between roars. Just before each roar there is a deep inhalation; the body is inflated and the throat puffed out. During the subsequent exhalation the entire body cavity is contracted in a series of powerful, spasmodic jerks. It is during the exhalation that the head and tail are raised highest out of the water. Each roar lasts for approximately one second according to Harper and 3.5 to 7 seconds according to McIlhenny. After the roar the head and tail are lowered, and the central portions of the body rise. In Harper's experience the next roar follows after an interval of two to three seconds, and there are very few repetitions. McIlhenny estimated the interval between roars to be about two minutes and reported that in some instances 12 or more roars were emitted in succession. The alternate sinking and rising of the body is probably related to changes in specific gravity accompanying inflation and deflation of the lungs (Harper, 1930).

When the head is raised out of the water, musk glands situated in the skin of the lower jaw are opened (Ditmars, 1910); and McIlhenny (1935) describes the "sweet pungent musk [which] scents the air and water and lingers for several hours."

ROARING IN A CAPTIVE ALLIGATOR

Four male alligators (*mississippiensis*) were maintained for several years in the laboratories of the Department of Animal Behavior at the American Museum of Natural

History. These animals had been given to the museum by tourists who purchased them during trips to Florida. In view of the fact that such specimens are usually sold while they are quite small it is probable that none of our alligators had had any extensive contact with wild adults of their own species. The reptiles ranged in length from 2 feet 4 inches to 5 feet 1 inch. Since alligators are about 8 to 10 inches long at hatching, and grow approximately 12 inches a year (McIlhenny, 1935), it is likely that the oldest of our animals was somewhat over five years of age. During the early stages of their captivity at the museum all four alligators were kept in the same tank and fed fish and beef heart three times a week.

The three smaller reptiles not infrequently emitted a call consisting of a series of short grunts, which might be written "umph! umph! umph!," and seemed to be elicited by contact with other alligators. So far as we could see the animals made no response when this sound was given by one of their number. The largest alligator could easily be induced to give a loud, prolonged "hiss," and this sound was evoked by noxious stimuli of various sorts such as poking the animal with a stick, turning a blast of air in his face or pouring water into the tank near his head. When the "hiss" occurs the alligator's mouth is held partly open, exposing the teeth. Although some of the smaller alligators were stimulated to "hiss" upon a few occasions the reaction was most easily and frequently evoked in the largest reptile.

After the alligators had been in the laboratory, approximately two years it was accidentally discovered that the largest animal (but none of the others) could be stimulated to roar in response to a particular sound. Following this discovery various tests were conducted one day each week for 18 weeks (January 8 to May 21) to obtain data for a detailed description of the reptile's response to tones of different frequency and quality.² The results

² Miss Eleanor Herrick's assistance in the conduction of these tests is gratefully acknowledged.

are less complete than we would wish, for it became necessary to discontinue the testing temporarily, and before observations could be resumed the alligator died. Since there is no immediate opportunity for extending the investigations we are reporting our incomplete data in the hope that they will prove of use to others who may be in a position to verify and extend them.

Original Effective Stimulus. In the museum laboratory are several glass-sided aquaria, the soapstone ends of which are connected on the outside of the glass by steel rods $\frac{1}{4}$ inch in diameter and 3 feet in length. Both ends of each rod are threaded, and nuts fastened on the outside of the stone ends are tightened to hold the stone firmly against the ends of the glass sides. Accordingly, the slender rods are always under considerable tension; and when one is plucked like the string of a musical instrument it vibrates for several seconds, producing a deep-toned, thrumming sound. It was in response to this sound that we first accidentally elicited roaring in the largest of the four alligators.³

Following our discovery of the reptile's responsiveness to this type of auditory stimulation he was transferred to a separate tank 17 feet long, 29 inches wide and 23 inches deep. Approximately 8 inches of water was kept in the tank and the room temperature was held at $80^\circ \pm 1$ F. Under these conditions the alligator's reactions to vibrations of the steel rod were tested one day each week for 11 successive weeks. Roaring occurred several times on each test day, although it was not evoked every time that the rod was activated.

Preliminary tests revealed that roaring was elicited when the rod was plucked once every 5 to 10 seconds and allowed to vibrate freely during the intervals. Activat-

³ In preparing this report we have assumed that the effective stimulus was exclusively auditory. There is of course some possibility (which we consider remote) that the animal responded to tactile stimulation arising from vibrations of the substratum. It seems to us that conditions of the various tests render such an interpretation unlikely; but the absence of a strict control of the vibratory factor should be noted.

ing the rod repeatedly at shorter intervals produced a steady volume of sound which failed to evoke the response; and plucking the rod once a minute or less frequently was equally ineffective. In all subsequent tests the rod was plucked at 5 to 10 second intervals until the first roar sounded or until it was judged that no response was going to occur. The initial roar was usually given after the rod had been activated 2 to 8 times; but under special conditions as many as 72 applications of the stimulus were necessary to call out the response, and in occasional tests no vocalization occurred.

Bodily Changes Accompanying Roaring. Analysis of motion pictures which were taken while the alligator roared provides the basis for a detailed description of the postural changes occurring during production of the roar. At the beginning of the first roar the alligator's head is raised above the water, and as inhalation occurs the sides swell noticeably and the central portions of the body, becoming more buoyant, rise. The subsequent exhalation, which is responsible for the production of sound, starts with a general compression of the lateral body walls in which muscular contraction appears to be fairly evenly distributed along the sides between the front and rear legs. This brief, initial contraction is followed immediately by spasmodic compression of the anterior portion of the sides just behind the forelimbs, with concomitant inflation of the more posterior sections of the lateral body wall. It is as though the extreme contraction in the thoracic area resulted in displacement of internal organs, temporarily forcing them posteriorly to distend the lateral abdominal wall.

The force of the second contraction is often sufficient to drive the animal backward in the water. This second and more powerful phase of the bodily contraction is accompanied by a sharp increase in the elevation of the head and a marked downward movement of the central portions of the body. Several roars usually occur in sequence, and with each succeeding vocalization the head is raised

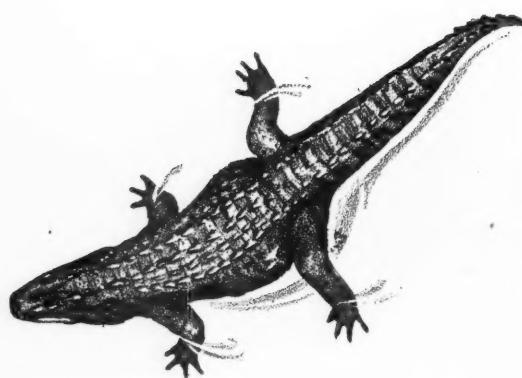
higher, so that after several roars it is at a sharp angle with the line of the back. During roaring there is a pronounced tendency to raise the anterior parts of the body by extending the front legs; and in connection with the most extreme roars the tail is raised slightly above the surface of the water. At the conclusion of the last roar the alligator may relax at once, lowering the head to the water level; but in the majority of instances the extreme elevation of the head and extension of the forelimbs is maintained in a motionless pose for several minutes. In 21 tests the pose was held for an average of 5 minutes after the final roar, and in a few cases the interval between the cessation of vocalization and general relaxation was longer (maximum 16 minutes). The various postural changes associated with roaring are illustrated in Fig. 1.

The postural changes described above accompanied roaring in almost every instance, but they are not inevitable and essential concomitants of the vocal response, for upon rare occasions roars were delivered when the alligator was lying nearly flat in the water or standing with the legs fully extended so that the body was raised as high as possible and held parallel to the water.

Our observations were made while the alligator was in approximately 8 inches of water which failed to cover his back; whereas the descriptions of roaring recorded by Harper (1930) and McIlhenny (1935) were based upon the behavior of swimming animals. Considering the differences in conditions under which observation occurred our account agrees closely with those of the earlier workers, and we are convinced that had our animal been tested in deeper water the pattern would have been identical with the behavior observed in the wild.

At no time was there any indication that our animal released the musk which is said to be emitted by wild alligators when they roar.

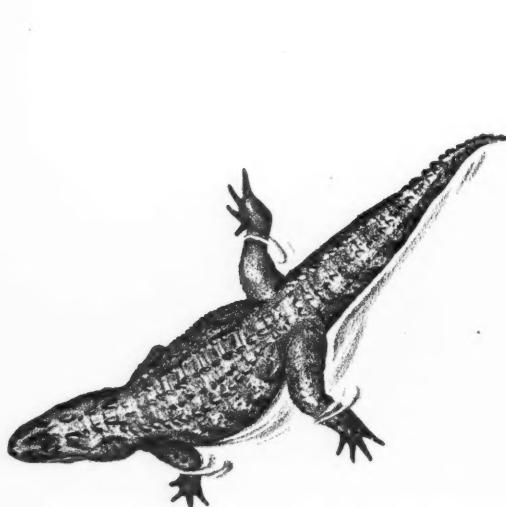
Occasionally when the alligator inhales preparatory to roaring there occurs a short "hic" sound just at the end



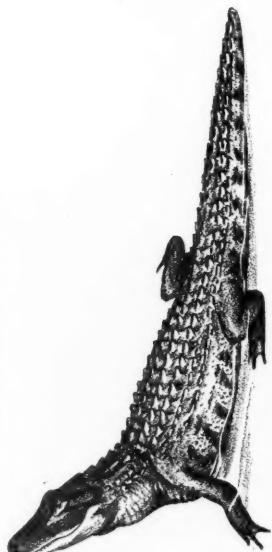
FINAL EXHALATION—DORSAL VIEW



FINAL EXHALATION—LATERAL VIEW



PRELIMINARY INHALATION—DORSAL VIEW



PRELIMINARY INHALATION—LATERAL VIEW

of the inhalation. Each of the two phases of the muscular contraction accompanying exhalation produces a distinct sound. The initial, general compression of the sides produces a moderately loud, deep note; and as the subsequent extreme lateral contraction of the anterior body cavity occurs the volume of this beginning note is suddenly, tremendously increased in very sharp crescendo, and at the same time the pitch rises appreciably. After coming suddenly to its peak the volume of sound dies out slowly and the pitch falls concomitantly. The entire roar lasts approximately one second and the beginning note takes up only the first one-fifth of this period. (Harper estimated the duration of the roar to be one second.) The alligator's mouth is opened less than $\frac{1}{2}$ inch if at all during inhalation and subsequent emission of the roar.

Frequency of Roaring. The alligator's reactions to the vibrating steel rod were observed one day each week for 11 weeks; and several tests were given each day. The rod was plucked at 5-second intervals until the first roar was elicited, and usually several successive roars then occurred without further stimulation. In 30 tests the number of consecutive roars varied from one to ten with an average of 7.4, but each of the extreme values occurred only once; and in 24 of the 30 instances the range was 6-8. When several roars were uttered in succession the intra-roar interval, as measured in 22 tests, ranged from 4.5 to 6.5 seconds. (Harper's estimation of the interval was 2 to 3 seconds.) In three instances longer intervals were recorded but these were unusual.

Occasionally the auditory stimulus was applied without eliciting any vocal response; but this usually occurred when a positive reaction had been obtained a short time before. To test the possibility that a series of roars is followed by a refractory period during which responsiveness to the auditory stimulus is reduced we attempted to exhaust the response by repeated stimulations. The rod was plucked until roaring began, and as soon as the alligator ceased roaring and relaxed, stimulation was re-

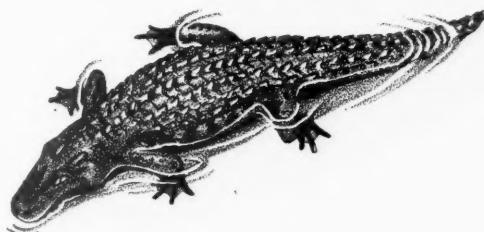
sumed. This process was repeated 5 times. The number of rod-activations necessary to evoke roaring in each successive instance was as follows: 26, 7, 47, 72, 51. We have here a rough indication that the response may become more difficult to obtain in successive tests which are very closely spaced. It is interesting to note, however, that the number of roars elicited by successive stimulations shows no tendency to diminish. The total number of roars sounded in each of these 5 tests was: 8, 6, 6, 7, 8. The number of roars that occur in a given response is apparently independent of the number of times the stimulus is applied before roaring begins. These findings suggest that roaring may be somewhat of an all-or-none reaction, and that a threshold phenomenon is involved.

Behavioral Changes Accompanying Roaring. Upon several occasions the alligator was tested in dim light. Before auditory stimulation began the vertical, slit-like pupil of the eye was always partially contracted, but after roaring it was invariably maximally expanded into a broad oval. Involvement of the autonomic nervous system is indicated. There were many other indications that the alligator was highly excited by the auditory stimulus. Under ordinary conditions he was extremely lethargic and unresponsive to environmental stimuli. Frequently when the rod was vibrated the alligator rushed to a point in the tank closest to the stimulus and slashed his tail back and forth several times before roaring. In many tests the animal repeatedly tried to force himself up and over the side of the tank, and these attempts were always made at the point nearest the position of the vibrating rod. When stimulation was resumed immediately after roaring ceased the reptile's apparent agitation increased, and he moved rapidly back and forth shoving against the wall of the tank nearest the stimulus and thrashing his tail rapidly from side to side.

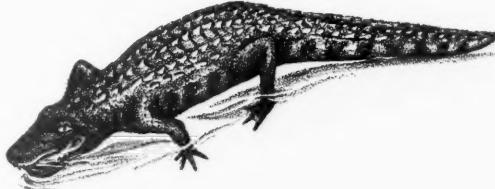
In some tests the manner in which the alligator moved toward the source of sound involved the adoption of a distinctive posture and method of locomotion which for

conveninence we have termed the "aggressive approach." In this behavior pattern the body is raised as high as full extension of all four limbs will permit; and as the animal walks the stepping reactions are slow and deliberate. The head and tail are held low, and elevation of the central portions of the body produces a distinct, convex arching of the back. The lateral body walls are dis-

TWO TYPES OF LOCOMOTION IN *ALLIGATOR MISSISSIPIENSIS*



USUAL WALKING POSTURE



"AGGRESSIVE APPROACH" POSTURE

FIG. 2.

tended to the fullest extent, appreciably increasing the animal's girth; and frequently when this posture is assumed the mouth is held half open. The postures of the alligator during the "aggressive approach" and during the more common type of locomotion, in which the body is low in the water, are shown in Fig. 2.

The "high walk" of the alligator has been compared by Schaeffer (1941) to the type of locomotion which

was probably exhibited by advanced therapsids such as *Bauria*. Both Schaeffer and Huene (1913) refer to the "high walk" in alligators and crocodiles as a method of rapid locomotion in contrast to the slower rate of progression achieved by walking with the limbs spread out and ventral surfaces dragging on the ground. Our observations indicate that when it is employed in the "aggressive approach" the "high walk" of the alligator is performed, not rapidly, but with very slow and deliberate movements.

Localization of the Source of Sound. In addition to roaring when the steel rod was vibrated the alligator made various responses which revealed his ability not only to hear but to localize the sound. In the majority of tests when the vibrating rod was employed the alligator moved to a position in the tank as close as possible to the source of the sound. Upon many occasions this reaction involved moving the full length of the tank (17 feet). Usually the approach was made before roaring occurred; but occasionally the roar was given and then the animal relaxed and moved swiftly to the source of stimulation. In one instance when the stimulus was presented the full length of the tank away from the alligator he roared without changing position and then, as the stimulation was resumed, moved quickly down to the other end and roared again.

In another test the rod was vibrated constantly while it was moved (on a small truck) from one end of the tank to the other and back again several times. The apparatus and the experimenter were well below the top of the sides of the alligator's tank, and thus completely beyond his visual field. As the vibrating rod passed back and forth on the outside of the tank the animal moved parallel with it on the inside. No roaring occurred, but the alligator followed the invisible stimulus closely without interruption for 10 minutes, and throughout this period he made repeated and vigorous attempts to raise his body to the top of the tank wall.

In tests to be described below several types of auditory stimuli were employed which did not elicit roaring, but in many instances the alligator's reactions conclusively demonstrated his ability to localize these sounds. Sometimes the animal moved part way to the source of stimulation, and in other tests the head was raised and turned toward the sound.

Although it seemed obvious that the alligator's vocal response and localizing reactions depended exclusively upon auditory stimulation a special test was conducted to rule out all possible visual cues. The animal's tank was completely covered with heavy black tar paper; yet under these conditions when the steel rod was vibrated roaring occurred promptly. The test was repeated several times with positive results, and when the tank covering was removed immediately after the final roar it was found that the alligator had moved as close as possible to the source of sound.

Since McIlhenny (1935) stated that he had never observed alligators roaring unless they were at least partly in the water, we conducted two tests to determine whether the response could be evoked with the animal in a dry tank. The tank was drained and the stimulus of the vibrating rod applied. The reptile roared readily in both tests and his behavior did not appear to be affected by the absence of water. In one test he showed the "aggressive approach" and came directly to the source of stimulation.

Response to Other Types of Auditory Stimuli. In all the observations described above a single type of auditory stimulation was employed, namely, the sound produced by the vibrating rod. Additional tests were conducted to determine the alligator's reactions to other sounds. The results of the supplementary experiments indicated that roaring could be evoked only by auditory stimuli of rather specific frequencies, namely, frequencies near that of the animal's own roar, or the first harmonic thereof.

Loud noises of various types were used in several tests without eliciting any observable response. Repeated

stimulations with a large electric buzzer or an electric bell sounded separately and simultaneously elicited no behavioral reactions.⁴ Tuning forks with frequencies varying from 256~ to 4098~ were used as stimuli on two test days.⁵ The forks were vibrated singly and in various combinations but in no instance did the alligator give any observable response.

By comparing the sound of the vibrating rod with the various notes on the diatonic scale we determined that, although many partials or harmonics were audible, the fundamental note was approximately equal to B flat two octaves below middle C. This note, which seemed to have roughly the same pitch as the alligator's roar, is produced by 57 vibrations per second.⁶ Unfortunately no apparatus was available which would produce pure tones of low frequency and high volume. As a substitute measure we investigated the possibility of using as a source of stimulation tones produced by various musical instruments; and after some exploration it was found that a sound closely resembling that emitted by the rod could be produced on the French horn. Accordingly, the reactions of the alligator to the tones of this instrument were tested.

The animal was stimulated to roar when a note produced by 57~ (B_b 2 octaves below middle C) was blown at 5-second intervals with a 2-second rest after each note. If the same tone was sounded continuously no roaring occurred. This tone, sounded at intervals, was used as a stimulus in 10 tests and roaring was produced in every instance. The animal's reactions to the 57~ tone of the French horn were the same as those given to the vibrating steel rod. Postural changes, evidence of excitement and

⁴ There have come to our attention anecdotal accounts of alligators roaring after a shotgun had been fired close by. None of our stimuli was as loud as a gunshot, and there is a possibility that greater volume would have proven effective in eliciting the roar.

⁵ The exact frequencies tested were as follows: 256, 320, 512, 640, 768, 896, 1,024, 1,152, 2,048 and 4,098.

⁶ All the frequencies mentioned in this report are approximate, but the maximum error is not more than 2 vibrations per second in either direction.

accurate localizing behavior were identical for the two types of stimuli.

Other tones with frequencies close to $57\sim$ failed to evoke roaring, but the reaction was elicited with some difficulty in response to the first harmonic of $57\sim$, namely $113\sim$ (B_{\flat} 1 octave below middle C). This note was used in 5 tests and roaring occurred in only one, indicating that the higher frequency (first harmonic) was less effective than the lower (fundamental). In 2 tests although the reptile did not roar in response to $113\sim$ he did move

TABLE I
RESPONSES OF AN AMERICAN ALLIGATOR TO VARIOUS TONES PRODUCED
BY THE FRENCH HORN

Auditory stimulus		Vibrations per second	Behavior of alligator
Note on diatonic scale			
B_{\flat} 2 octaves below middle C	57		Roared in every test
A and B_{\flat} trill 1 octave below middle C	107 + 113		Opened mouth widely
B_{\flat} 1 octave below middle C	113		Roared in 1 test; localized source of sound in all other tests
A and B_{\flat} trill immediately below middle C	213 + 227		Hissed
B_{\flat} immediately below middle C	227		Raised head; came to source of sound; hissed
E and F trill above middle C	320 + 341		Moved head toward sound; hissed
A and B_{\flat} trill 1 octave above middle C	426 + 453		None

toward the source of sound. No other tone or combination of tones produced by the French horn stimulated roaring, but several frequencies elicited behavioral responses indicating that they were within the animal's auditory range. A list of the frequencies tested with notes on behavior is presented in Table I.

The various tones were not tested extensively, but there appears to be sufficient evidence to indicate that the alligator was sensitive to a greater or less degree to frequencies between $57\sim$ and $341\sim$; and that roaring occurred most readily in response to $57\sim$, although it could occa-

sionally be elicited by the first harmonic of that frequency. It should be noted that tuning forks with frequencies of $256\sim$ and $320\sim$ elicited no response on the part of the alligator, whereas tones of the French horn within this range, although this did not induce roaring, did prove audible to the animal. It seems likely that differences in volume or in the quality of the stimulus were responsible for this difference in responsiveness.

To determine the possible effects of varying the quality of the stimulus while holding the frequency constant we tested the response of the alligator to various notes played on a 'cello. The frequencies which had proven effective in the case of the French horn were found capable of evoking roaring when the stringed instrument was employed as the source of sound. A note of $57\sim$ played at 5 second intervals always stimulated the animal to roar (3 tests), and a tone one octave higher ($113\sim$) induced this reaction occasionally. Other notes or combination of notes failed to call forth any vocal response.

Response to Phonographic Recordings. Phonographic recordings were made of the alligator's roar and of the sound of the vibrating steel rod and the French horn (blown at $57\sim$). The fidelity of reproduction was not high, but recordings of the French horn and of the alligator's own roar called forth answering roars in several tests; and in every instance the animal appeared to be highly excited, moving rapidly up and down the tank with his tail slashing in a wide arc, and frequently assuming the "aggressive approach" posture. When the record of the rod's vibration was played on a small portable phonograph the animal hissed several times, but failed to roar.

BEHAVIOR TOWARD OTHER ALLIGATORS

It is generally agreed (True, 1893; Reese, 1907; Harper, 1930; McIlhenny, 1935) that alligators roar most frequently during breeding season, and it is at this time particularly that males are strongly aggressive and fight

among themselves a great deal. Since roaring seems to be associated with certain types of social behavior, and since our animal gave evidence of being highly excited when he was stimulated to roar, it was of interest to investigate his reactions to another alligator during tests in which the effective auditory stimulus was applied. Accordingly, during 4 different test days we placed the second largest animal (length, 4 feet 10 inches) in the tank with the male who roared. On the first 2 test days each time the large alligator roared the smaller animal approached him uttering the "umph!" sound described earlier. The larger reptile seemed to pay no attention to the smaller, and often crawled over him while moving toward the source of auditory stimulation. Upon such occasions the smaller alligator gave no evidence of being excited, but emitted the "umph!" call when touched.

On the third test day the large alligator was stimulated to roar and immediately thereafter the smaller individual was introduced into the tank. The larger animal at once assumed the "aggressive approach" posture and moved toward the smaller male. The large reptile halted about 18 inches away from the other alligator maintaining the aggressive pose, and the smaller individual, who had retreated into one corner of the tank, slashed his tail rapidly from side to side whereupon the large alligator backed away and relaxed. Several times thereafter the large male advanced upon the smaller employing the "aggressive approach." In each instance the smaller male fled to the farthest end of the tank, but the aggressor pressed his advantage only so far, always halting before actual contact was established.

Approximately one month later the smaller alligator was returned to the larger animal's tank for a fourth test and the latter immediately showed the "aggressive approach." In this case, as in the preceding test, the smaller reptile appeared to be highly excited by the "aggressive approach" of the other male and moved quickly to the far end of the tank. The larger alligator pursued,

cornered the other animal in one end of the narrow tank, made a final lunge and bit him severely. The smaller individual slipped past the attacking male, but was pursued and bitten again. This type of interaction between the two alligators was repeated several times with the larger animal always assuming the aggressive rôle and the smaller individual seeking only to escape. The large male's attack was not restricted to any particular part of the smaller alligator's body; but head, limbs and tail were seized and bitten indiscriminately.

The largest male's tendency to attack a second alligator was quite probably related to general excitement resulting from auditory stimulation presented earlier on the same days; and in addition tonal stimuli delivered while the second animal was in the tank appeared to increase the frequency of the "aggressive approach." However a close temporal relationship between roaring and attack was not apparent. It is possible that some sort of "territory defense" was also involved. For more than a year prior to the experiments herein reported all four alligators had been kept together in one tank and no fighting occurred at any time. Then for several months the largest individual lived alone in a much larger space. It is not unlikely that his attacks upon the second male suddenly introduced into his solitary tank were in the nature of territory defense intensified somewhat by auditory stimulation. Harper (1930) has pointed out that adult alligators in the wild often live in small "'gator holes'" and suggests that they "probably exercise some sort of proprietary rights over [their] home territory."

To determine whether any territorial behavior could be elicited the four alligators were released in an outdoor pen 24 feet square. One corner of the area was flooded to form a pool some 15 feet across and 6 to 12 inches deep. Although they lived in the large pen for more than a month none of the animals showed any tendency to establish individual territories. On the contrary, they usually stayed close together, sometimes in the water and some-

times in the dry portions of the pen. When the observer approached, all four animals moved away and all but the smallest hissed. Upon 2 days while the alligators were outdoors the steel rod was vibrated in an attempt to induce roaring. At the first test the largest alligator approached the sound, then went into the water and roared. Upon other occasions he made no response unless the stimulus was within a few feet, in which case roaring occurred. Under these conditions no aggressive reactions toward other alligators were observed.

ROARING IN A SECOND ALLIGATOR

Only one of the four alligators in the Museum laboratory could be induced to roar in response to an auditory stimulus. Since the other three individuals were smaller and undoubtedly younger we wished to repeat our tests using another large alligator. A single series of observations was conducted at the New York Aquarium through the courtesy of its director, Dr. C. M. Breder. In the large indoor pool were five *Alligator mississippiensis*, one Chinese alligator (*A. sinensis*) and one American crocodile (*C. acutus*). Recordings of the roar emitted by the alligator at the Museum and of the sound produced by the vibrating steel rod were played at the Aquarium, but the sound was very weak in a large room and the only response elicited was some head movement on the part of two *A. mississippiensis*.

The French horn was blown at 5-second intervals (frequency 57~) for several minutes, and the largest *Alligator mississippiensis* roared twice in reply. The test was repeated 3 times and 4 roars occurred in each test. None of the other animals gave any vocal reactions, but several of them swam toward the sound.

The alligator which roared in response to the French horn was larger than the Museum animal (approximately 7 feet in length) and his roar was of lower pitch. After several roars had occurred the pupil of the eye was noticeably dilated. At the Aquarium the alligators swam in

water several feet deep, and this resulted in somewhat different postural adjustments during roaring. The head was elevated at a sharp angle; the back was concavely arched; and the tail was raised out of the water with the tip bending downward to touch the surface. Each time the animal roared the strong contraction in the lateral thoracic region resulted in a marked downward movement of the body, and the following inhalation raised the body again; so that as a series of roars was emitted the alligator bobbed up and down in the water repeatedly. This description agrees closely with those of Harper (1930) and of McIlhenny (1935) who observed the behavior in wild alligators; although the emission of musk reported by these writers was not observed in the case of the Aquarium specimen.

DISCUSSION

Controlled laboratory experiments have shown that many amphibia respond to air-borne sounds (Yerkes, 1905; Bruyn and Van Nifterick, 1920; Patterson, 1920); and field observations indicate that auditory stimuli play an important rôle in the lives of some frogs and toads (Noble, 1931). There is a good deal of evidence to suggest that a true auditory sensitivity is lacking in most reptilian species. Kuroda (1923), working with the Japanese pond turtle (*Clemmys japonica*), was unable to obtain any reaction to sounds; and other turtles, tortoises and snakes are apparently equally unresponsive to auditory stimulation (Beatty, 1932; Evans, 1935b). Studies of electrical activity in the eighth nerve support the conclusions based upon observations of behavior. In the grass snake (*Natrix natrix*) loud sounds produce no activity in the eighth nerve; and in the common land tortoise and the box tortoise (*Terrapene*), although action currents occur when the ear is exposed to sound, the currents in the nerve are due entirely to action potentials in its fibers and the animals "give no sign of appreciating the sounds to which their ears are sensitive" (Adrian, 1938).

Several observers have noted that some lizards are sensitive to sounds. Kuroda (1923) found that *Tachydromus tachydromoidae* shows a modification of certain visual reflexes when stimulated with a bell or with a Galton whistle. According to Beatty (1932) the green lizard (*Lacerta viridis*) responds to auditory stimuli; and Berger found that *Lacerta agilis* and *L. vipipara* exhibited specific eye reflexes, modified their respiratory rhythm, and could be trained to execute learned responses to loud noises as well as tonal stimuli.

The alligators and crocodiles have a membranous ear drum, a true cochlea (Adrian, 1938) and a tectorial membrane (Evans, 1935b); and in the alligator a true Wever and Bray effect is obtainable. As in birds and mammals electrical oscillations corresponding in frequency to the sound stimulus can be picked up from any part of the inner ear, and cochlear potentials spread into the eighth nerve (Adrian, 1938). Thus the anatomic and physiological basis for hearing is present.

Evans (1935b) has pointed out some interesting correlations between the proportions of certain inner ear structures and the presence or absence of "vocality." He emphasizes the fact that among the amniotes good evidence for vocality is available only for gecko lizards, alligators, birds and mammals. Turtles, snakes and all lizards except geckos are non-vocal according to Evans (since hissing is not accepted as "true vocality"). When the length of the cochlea is compared to that of the lagena the ratio is found to be 0.5:1 in turtles (4 species), 0.5:1 in snakes (5 species), and 1.28:1 in all lizards except skinks and geckos (8 species). Relative cochlear length is increased in the skink so that the cochlea/lagena ratio is 2.64:1, and in this group vocality may exist, although this is not certain. In geckos (*Gymnodactylus kotschy* and *Hemidactylus turcicus*) the ratio becomes 3.2:1; and these species are quite vocal, employing their calls especially during breeding season. The alligator has a cochlea/lagena length ratio of 4.7:1, and is known to

vocalize extensively under certain conditions. Evans concludes that "the cochlea must bear a length ratio of 3:1 to the lagena before any amniote is capable of modifying its social behavior (particularly fighting and mating) by means of vocalicity."

Field observations strongly suggest that in the alligator vocal expression forms an integral part of certain behavior patterns, but there is a paucity of experimental evidence regarding either audition or vocalization in alligators or crocodiles. Reese (1923) tested the response of *A. mississippiensis* to thermal, visual, chemical and gravitational stimuli, but gives no evidence regarding effects of sound impulses. Berger (1924) found that the West African short-snouted crocodile (*Osteolaemus tetraspis*) altered its rate of breathing in response to the sound of an electric bell, a siren or the firing of a blank cartridge. Present results suggest that *A. mississippiensis* is capable of hearing sounds between 57~ and 341~, and since other frequencies were not explored the range of sensitivity may be much greater than these values would indicate. Furthermore, the animal's ability to localize accurately the source of auditory stimulation seems clearly established by our data.

Results of this investigation appear to have some bearing upon the interpretation of possible functions of the vocal response. Various observers have stated that when one adult bull alligator roars others will reply; and our laboratory tests (particularly those involving the response to a recording of the roar) give support to this conclusion. It will be recalled that the roar has been variously interpreted as a mating call by which the females are attracted to the male (Harper, 1930), and as a challenge to other adult males (McIlhenny, 1935). In this connection the behavioral responses of our specimen to 57~ stimulus are of particular interest. In nearly every instance the male moved as close as possible to the source of the sound; and in many tests the method of progression involved the display of the "aggressive approach."

The "aggressive approach" pattern in the alligator is strikingly similar to the postural responses shown by some lizards during fighting and/or preliminary courtship. The male eastern whip-tailed lizard (*Cnemidophorus sexlineatus*) when approached by another lizard rises high on his legs, automatically displaying his bright, blue ventral surfaces. A similar reaction is made by the eastern fence-lizard (*Sceloporus undulatus*); and this type of behavior has been interpreted as assisting in sex recognition, since it is usually shown only by the male (Noble and Bradley, 1933). In fighting, the western banded gecko (*Coleonyx variegatus* Baird) rises high on all four legs, arches his back and holds his head low (Greenberg, 1943). The male American chameleon (*Anolis carolinensis*) raises his body as high as possible prior to attacking other males (Evans, 1935a).

The manner in which the alligator that we observed approached the source of stimulation and the nature of his subsequent reactions to a second male lead us to suspect that the auditory stimulation and the resultant vocalization were associated with emotional excitement and an increased tendency toward actively aggressive behavior. It seems probable that under natural conditions the roars of the breeding male are likely to arouse aggressive responses in other males, and possibly to increase fighting since other alligators may seek out the vocal individual. It is of course also conceivable that females tend to approach roaring males, but the evaluation of this possibility must await further evidence.

SUMMARY

A male *Alligator mississippiensis* (5 feet 4 inches long) was stimulated to roar in response to a tone of approximately $57\sim$, and occasionally by the first harmonic of this fundamental. Other tones ranging upwards to $341\sim$ failed to elicit roaring but did evoke behavioral changes indicating the animal's auditory sensitivity. Three smaller males did not roar, but gave evidence that the

sounds were heard. Roaring was accompanied by accurate localizing responses and by the adoption of an "aggressive approach" type of locomotion; and a smaller male was attacked repeatedly when placed in the tank with the roaring alligator. Bodily changes during roaring have been described and the bearing of present observations upon reports by field naturalists discussed.

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HORN AND SCUR INHERITANCE IN CERTAIN BREEDS OF SHEEP¹

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WARWICK and Dunkle (1939) and Ibsen and Cox (1940) have written papers devoted to the inheritance of horns (and their absence) in sheep. The present paper is a fairly extensive revision of that by Ibsen and Cox and is based chiefly on a thorough analysis of the results of Arkell (1912) and Wood (1905, 1909). Arkell, especially, gave many details which will be utilized here but which were either not interpreted or were misinterpreted. The increase in knowledge of genetics enables one to make new interpretations with a definite assurance that they fit the facts more nearly than do the older theories.

Although the results of Arkell and of Wood are extensive, they are not by any means complete enough to fully substantiate the interpretation herein presented. Sheep are being produced at most of our agricultural experiment stations, and are under the control of men many of whom are well versed in genetics. With a working hypothesis such as the one presented here, and with others like that of Warwick and Dunkle (1939), these sheepmen should be better able to collect crucial data bearing on horn inheritance in sheep. Some of the data may be obtained in routine breeding operations, and the remainder by planned crosses.

It seems reasonable to suppose that by having a complete knowledge of the mode of inheritance of horns, etc., in sheep, cattle, goats and other horned animals, one will have important facts bearing on the question of organic evolution.

¹ Contribution No. 147 from the Department of Animal Husbandry. Most of the experimental results in this paper are from the publications of Arkell (1912) and Wood (1905, 1909). It would require too much space to show in detail how their data fit in with the mode of inheritance herein suggested. A longer paper showing this relationship has been written, and has been placed on file with the Wistar Institute, Philadelphia. The latter has kindly consented to loan this copy to those wishing for more detailed information.

Before going into detail concerning the various characters inherited, it seems advisable to describe the pure breeds that have entered into the various crosses. In the United States there are three main types of pure breeds. (1) Those in which both sexes are hornless (also called "polled"), consisting of Southdowns, Shropshires, Hampshires and, more recently, Suffolks. All are originally from England. (2) Those in which the male is horned and the female polled. The most common breed is the Rambouillet, which, in turn, is one of several making up what are called Merinos. The latter were originally Spanish, and the Rambouillets are a French variant produced by selection. (3) Those in which both sexes are horned, the male having larger horns than the female. The Dorset Horn, coming originally from England, is the most important breed of this type.

Certain variations occur within the pure breeds. In the breeds polled in both sexes, such as Southdowns and Suffolks, a small percentage of the males develop seurs (short, hornlike growths) as they grow older. No seurs are known to develop in Southdown females, but, on the other hand, a very small number has been reported in Suffolk females. For many years it was assumed that the presence of seurs was an indication of heterozygosity. The polled condition (*P*) is dominant to horned (*p*), and seurs were thought to be found only in *Pp* males. Disproof for this theory is found in the fact that no horned (*pp*) animals are ever found in purebred Southdowns, Shropshires and Hampshires. Therefore these breeds must be *PP*. One horned animal, reported in Suffolks, will be discussed later. It seems more appropriate to assume that seurs are due to a separate gene (*Sc*), which is partially sex-limited and is epistatic to *P*. Further details concerning their inheritance will be discussed in the body of the paper.

In Rambouillets, where the male is horned and the female hornless, two variations may be mentioned. The most common is the presence of seurs in the females. The

gene (*Sr*) producing these scurs will be shown to be different from that producing scurs in polled breeds (*Sc*). The other variation in Rambouilletts is the presence of the polled condition in some of the males. Warwick and Dunkle (1939) have furnished proof that this is due to the same gene (*P*) that causes both sexes to be polled in Southdowns, etc. Warwick and co-workers (1939) have also found that one of their polled Rambouillet males has scurs, even though his composition is *PP*, thus furnishing additional evidence that scurs are not the result of heterozygosis.

All Dorset Horns are horned in both sexes, and no apparent variations have been reported. There is evidence, however, that individuals within the breed differ in regard to the genes that they carry hypostatically. Such differences are demonstrated by means of the offspring obtained in crosses with other breeds. Further details are reserved for later discussion.

GENE INTERACTIONS

Warwick and Dunkle (1939) assume that the three types of breeds above enumerated differ from each other in regard to horn character by a single gene, the three genes forming an allelomorphic series. The evidence obtained thus far, however, does not preclude other explanations. The one offered here is that all sheep are homozygous for horned (*H*) and that two pairs of modifiers act on *H* to produce the three breed types. The factor pairs are *P* = polled, *p* = absence of *P*; *Hm* (dominant to *hm*), *hm*, a modifier which causes an otherwise horned female to be hornless. *P* is assumed to be epistatic to *H*. Thus a *PPHHmHm* (or *hmhm*) would be polled in both sexes, as is the case in Southdowns. A *ppHHmHm* would be horned in both sexes (as in Dorset Horned) and a *ppHHhmhm* would be horned in the males and hornless in the females, as in Rambouilletts. Both theories fit the facts so far as they are known at present. It would be necessary to run carefully planned experi-

ments before one could get definite evidence proving one theory and disproving the other. These will not be discussed here.

Except for the assumption that seurs are the result of incomplete dominance in *Pp* males, no other theory but that of Ibsen and Cox (1940) has been advanced to explain the inheritance of seurs in sheep. They assumed that one gene (*Sc*) could explain the presence of seurs both in the hornless breeds (such as Southdowns) and in Rambouillet females. A careful study of Arkell's (1912) data has since shown that a one-gene hypothesis will not hold for both cases. Each of the two kinds of seurs is due to a different gene. Thus *Sc* produces the seurs in polled breeds and *Sr* the seurs in Rambouillet females. The interaction of these genes with other genes will be given in greater detail.

The gene *Sc* is sex-limited to the extent that in polled individuals that are *Scsc* the seurs will show only in males. Thus *Sc* is epistatic to *P* in males. It is not definitely known whether or not seurs will show in polled females that are *ScSc*. Since the character is rare in such breeds as the Southdowns, in order to obtain *ScSc* females, it would be necessary for both parents to be *Scsc*, and in that case only one fourth of the female offspring would be of the required composition. Scurred females are not known in present-day Southdowns, Shropshires and Hampshires. On the other hand, in answer to a questionnaire that I sent out to a few Suffolk breeders, one replied that he had seen a Suffolk ewe with seurs. All the breeders were agreed that from 3 to 5 per cent. of the Suffolk males have seurs. If we assume that the scurred Suffolk female is *ScSc*, and that 5 per cent. of the Suffolk males are scurred (most of these would be *Scsc*), then the chances of producing a scurred female in the Suffolk breed would be approximately $.05 \times .05 \times .25 = .000625$, or about six in every 10,000 females. Since seurs occur less frequently in the males of the other polled breeds, there would be a very small chance of their occurring in the females of these breeds.

One other fact mentioned by a Suffolk breeder might be given at this time. In 1933 a ram in his flock was born which later grew fully developed horns "with a full turn around his ears." This same breeder states that Suffolks are descended from crosses between Southdowns (*PP*) and Norfolks (*pp*). Apparently the horned ram was from heterozygous (*Pp*) parents, thus demonstrating that the Suffolk has not as yet become completely homozygous for polled, in this respect differing from the Southdown and the other polled breeds mentioned.

Those who assume that scurs are the result of heterozygosis base it on the fact that in crosses between polled (in both sexes) and horned (in both sexes) breeds many of the male offspring have scurs. Some of the crossbred males have fairly long horns, and a few have neither horns nor scurs, being clean polled. Thus, if it were heterozygosis, it would be very irregularly expressed. In those crosses where the polled parent is either a Southdown, Shropshire or Hampshire, the female offspring are clean polled. But if a Suffolk is the polled parent, some of the daughters have scurs, as will be shown later in the discussion of Wood's (1905, 1909) results.

The explanation given here for the above results is that the horned parent may carry the scur gene (*Sc*) hypostatically (*ppHHS_cSc*). Surs will show in the *F*₁ males since *Sc* is epistatic to *P*. Assuming both parents to be homozygous, the cross would be as follows:

Polled	Horned	Males	Females
<i>PPHHscsc</i>	<i>ppHHS_cSc</i>	<i>PpHHscsc</i>	seurred polled

An analysis of Arkell's (1912) data reveals that there is a fairly sharp line of demarcation between those *F*₁ males that have scurs and those that have horns. The scurs are never more than two inches long, and the horns never less than four inches in length. The horns produced in the crossbred males are assumed to be due to a separate gene (*Ha*) which is epistatic to *P* and hypostatic to horns (*ppHH*). It corresponds to the *Ha* gene in cattle, described by White and Ibsen (1936). Arkell's

data are not extensive enough for one to determine whether or not *Sc* and *Ha* are allelomorphic. In the present discussion, *ha*, the allelomorph of *Ha*, is merely the absence of *Ha*. The latter will express itself in heterozygous males (*Haha*) that carry *P* (*PpHHHaha*), but females of this composition will be clean polled. It is not known whether *HaHa* "polled" females (*P-*) show horns. Arkell had one *F*₁ male that carried both *Sc* and *Ha*. It was scurred in appearance, thus demonstrating that *Sc* is epistatic to *Ha*. The presence of the *Ha* gene in this male was shown by the fact that he sired a horned male when mated to a purebred polled female (*PP*).

Arkell's (1912) data furnish satisfactory proof that his Rambouilletts carried both of the scur genes (*Sc* and *Sr*). The presence of the *Sc* gene was demonstrated by the fact that when purebred clean-polled males (*PPscsc*) were mated to clean-polled Rambouillet females (*ppHHhmhm*) some of the sons had scurs, the gene for which must have come from the mother. Thus we are forced to conclude that *Scsc* Rambouillet females are similar to *Scsc* females of the polled-in-both-sexes (*PP*) breeds in that scurs (due to *Sc*) do not show.

The scurs that do show in a Rambouillet female are caused by another gene, *Sr*, and the gene expresses itself even when the female is heterozygous (*Srsr*). Rambouillet females without scurs (but having two bony knobs on the skull) are of the composition *srsr*. Rambouillet males are typically horned, the *Sr* gene when present being hypostatic to the horned condition. By mating a Rambouillet male to scurless (*srsr*) Rambouillet females it should be possible to determine his composition in regard to *Sr*. One such male (J. K. Madsen 2886-E) in the Kansas State College flock proved to be *Srsr*. When mated to clean-polled Rambouillet females, seven of his daughters had scurs (*Srsr*) and six did not (*srsr*).

In the present discussion all sheep are postulated to be homozygous for *H*, the horn gene. Five pairs of allelomorphs have also been postulated to account for the vari-

ous "horn" conditions found in these animals. Thus it should be possible to give the genotype of the various breeds, taking all the genes into consideration. Those genes that are hypostatic in a particular breed are placed within parentheses.

The purebred polled-in-both-sexes breeds, such as the Southdowns, Shropshires and Hampshires, would be of the following composition, if neither sex showed any scurs:

$PPHH(HmHm, Hmhm, hmhm)hahascc(SrSr, Srsr, srsr)$

In the above genotype it is assumed that Sr is unable to express itself in the presence of P . If the male is scurred, the $scsc$ should be changed to $Scsc$.

Horned-in-both-sexes breeds, such as the Dorset Horn would be of the composition:

$ppHHHmHm(HaHa, Haha, haha)(ScSc, Scsc, scsc)(SrSr, Srsr, srsr)$

Some Dorset Horns have been shown by means of crosses to carry Ha and Sc , but none has ever been tested in regard to Sr . The test could be made by mating Dorset rams to scurless ($srsr$) Rambouillet females, and mating the crossbred rams back to scurless Rambouillet ewes. If any of the females produced from this last mating had scurs, it would be a fairly definite proof that the Sr gene came from the P_1 Rambouillet rams.

Purebred Rambouillets (males horned; females either hornless or scurred) would be:

$ppHHhmhm(HaHa, Haha, haha)(ScSc, Scsc, scsc)SrSr, Srsr, srsr$

Tests for the presence, or absence, of Ha and Sc can be made by means of crosses with PP breeds, such as the Southdown.

SUFFOLK SHEEP

Suffolks are hornless in both sexes, like Southdowns, Shropshires and Hampshires, and, like them, are of English origin. Nevertheless they are different in that they carry two dominant genes which are absent from the other three breeds. Suffolk sheep are comparatively recent importations to the United States, and have been gradually growing in popularity.

Both Arkell (1912) and Wood (1909) have reported on crosses of horned-in-both-sexes breeds with hornless-in-both-sexes breeds. Both experimenters used Dorset Horns as the horned breed, but Arkell used Southdowns, Shropshires and Hampshires as the polled breeds and Wood used only Suffolks. Wood's results were different from Arkell's and the cause seems to lie in the fact that Suffolks have certain peculiarities not found in other polled breeds.

For example, Wood (1909) and Marshall (1912) both state that scurs do not appear on Suffolk males until after they are one year old. Suffolk breeders in the United States, in answer to recent inquiries, report that 3 to 5 per cent. of Suffolk males have scurs, that some scurs appear early, and that others appear only after the animals are two years of age. Scurrs when present in Southdown, Shropshire and Hampshire males always appear early. The evidence for this last statement is not complete.

The results obtained in Wood's (1909) crosses with Dorset Horns also prove that Suffolks differ from Southdowns, Shropshires and Hampshires. Wood's Suffolks apparently were scur-less, like the above breeds, but, in reciprocal crosses with Dorset Horns, the F_1 males began at an early age to develop horns. Thirty-six of the males were castrated, and their horn growth stopped almost immediately. One can not be certain that these 36 would have developed horns instead of scurs if they had not been castrated, but at any rate the two uncastrated males developed horns. These horns would be due to *Ha*, and Wood's evidence, so far as it goes, points to the fact that castration inhibits the growth of *Ha* horns. Similar results have been obtained on castration of Rambouillet rams (Nordby, 1928). In Dorset Horn rams, on the other hand, castration causes a slowing up of horn growth, but not a complete cessation. Arkell's F_1 males (Dorset Horn \times Southdowns, Shropshires and Hampshires) were more variable than Wood's in that some had scurs and others, horns.

The greatest differences, however, were in the F_1 females. All Arkell's F_1 females were clean polled. All Wood's began to develop scurs in their second or third years. There were 28 F_1 females that lived to this age.

In order to explain the peculiarities within the pure-bred Suffolks, and also the results obtained in the F_1 and F_2 generations of crosses with horned breeds, it seems necessary to postulate that Suffolks carry two dominant genes that are not found in such polled breeds as the Southdowns, Shropshires and Hampshires. The first dominant gene (*Pe*) is one that postpones the expression in males of the *Sc* gene, but has no retarding effect on *Ha* horns in males. Before stating its effect in females it is necessary to describe the other dominant gene. This gene (*Su*) makes it possible for *Ha* to express itself in *Haha* females, thus preventing *Ha* from being partially sex-limited. It has been called *Su* because it is peculiar to the Suffolk breed. *Su-Ha-P-* females would thus tend to have horns. If *Pe* is present, however, (*Su-Ha-P-Pe-*), it delays the expression of the *Ha* gene in the female, with the result that the horns never get long, and are therefore described as scurs. It should be noted that both *Pe* and *Su* express themselves only in the presence of *P* (polled). There is no evidence concerning the effect of *Pe* on scurs in females.

Since the evidence indicates that the F_1 males and the F_1 females in Wood's crosses were uniform within each sex and, also, since the numbers were fairly large in each group, one is forced to conclude that his P_1 Suffolks and his P_1 Dorset Horns were both homozygous for a fairly large number of genes:

Suffolk	Dorset Horn
$(P_1) PPHHscschahaSuSuPePe \times ppHHS-Sc-HaHasusupepe =$	
$(F_1) PpHHS-Sc-HahaSusuPepe$	$\left\{ \begin{array}{l} \text{males, horned} \\ \text{females, scurs appear late} \end{array} \right.$

In the above cross *Sc* is represented as being present in the Dorset Horns. The evidence that *Sc* was carried by at least one of the P_1 pure breeds is found in the fact that two of the F_2 animals were scurred. It has previously

been shown that *Sc* is epistatic to *Ha*, and yet apparently all the F_1 males would have been horned. The reason for this is that the *Pe* gene has a delaying effect in males on *Sc*, but not on *Ha*.

Certain peculiar results obtained by Wood on back-crossing F_2 animals to P_1 can be explained by the above theory. A horned F_2 male mated to purebred Dorset Horns produced some horned offspring and one that was polled. Similar results were obtained when one of several horned F_2 females was mated to a purebred Dorset Horn. Under ordinary conditions one would expect both of the above horned parents to be recessives (*pp*), and that they thus would produce only horned offspring.

The evidence indicates that both F_2 horned animals are *PpHa-*. To explain the F_2 horned female one has to postulate that she is in addition at least *Susu* in order to permit *Ha* to express itself. She must also be *pepe*, otherwise the expression of the *Ha* gene would be postponed, and result eventually in scurs. The unexpected polled offspring from either cross would be *PpHHhahascsc* (*Susu, susu*) *pepe*.

SUMMARY

- (1) All sheep are postulated to be homozygous for *H*, the gene for horns.
- (2) The gene *P* (polled) is epistatic to *H*. Polled breeds are thus *PPHH* and horned breeds *ppHH*.
- (3) In what would otherwise be horned animals the gene *hm* (horn modifier) causes the female to be hornless. Thus a *ppHHhmhm* male is horned and the female hornless, as in Rambouillet. Animals of the composition *ppHHHmHm* would be horned in both sexes, as in Dorset Horns. *P* is epistatic to both *Hm* and *hm*.
- (4) The gene for scurs, *Sc*, is epistatic to *P*, but in heterozygous animals (*ScscP-HH*) it expresses itself only in the male. Homozygous females (*ScScP-HH*) probably are scurred. In horned animals, *Sc* is hypostatic whether it is in the homozygous or in the heterozygous condition (*ScScppHH*).

(5) Another gene for horns (*Ha*) is found in sheep. It differs from *H* in that it is epistatic to *P*. *Sc* is epistatic to *Ha*. Thus a *PpHHScscHaha* male would be scurred, while a *PpHHscscHaha* male would be horned. *Ha* apparently has no effect in a *ppHHHa*-(horned) animal.

(6) There is also another gene for scurs (*Sr*), found in Rambouillet females. It produces an effect in both heterozygotes (*Srsr*) and homozygotes (*SrSr*). Breeding tests have shown that some scurless (*srsr*) Rambouillet females may carry *Sc*, the other scur gene.

(7) Suffolk sheep, one of the hornless-in-both-sexes breeds, apparently carry two dominant genes that are not found in other hornless-in-both-sexes breeds, such as the Southdowns, Shropshires and Hampshires. The gene *Su* permits the horn gene, *Ha*, to express itself in heterozygous females (*Su-P-HHHahascsc*), thus causing *Ha* no longer to be partially sex-limited. The other gene, *Pe*, postpones the expression of the *Sc* gene in males and of the *Ha* gene in females. In *Su-Pe-P-HHHahascsc* females the expression of the *Ha* is postponed for over a year, and as a result the horns are so short that they are called scurs. In males of the same composition the horns, due to *Ha*, start growing immediately and therefore become large.

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THE SPADEFOOT TOADS IN OKLAHOMA WITH A SUMMARY OF OUR KNOWLEDGE OF THE GROUP¹

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THE first spadefoot was described by Harlan from South Carolina in 1835. Since then, seven others have been named, all from North America, the latest in 1910. Sometimes placed in the Old World family *Pelobatidae*, they are now more commonly considered as members of a separate group, the *Scaphiopodidae*, containing the single genus, *Scaphiopus*. This paper, therefore, deals with the eight taxonomic forms of this genus.

From the first, the spadefoot toads have stimulated great interest because of several peculiarities manifested by some or all of them: (1) some species are very secretive and shy and are seldom found in numbers and then only after long intervals of time; (2) the developmental rate of their embryos and larvae exceeds that of any commonly studied amphibian (Wright and Wright, 1933; Ortenburger and Ortenburger, 1926; Trowbridge and Trowbridge, 1937; Bragg, 1941c); (3) their distribution is not what might be expected from their structure; for, having a thin, rather soft, frog-like skin suggesting an aquatic or semiaquatic habitat, all are in reality as nearly terrestrial as amphibians usually become, and most of the species are limited to xeric habitats in grasslands and deserts; and (4) the details of their taxonomic relationships have, till quite recently, been in confusion due in part to lack of specimens, in part to so few herpetologists having had opportunity to study them in their native haunts, and in part to a dearth of information on their tadpoles and life histories.

¹ Observations on the Ecology and Natural History of Anura. XII. Contribution from the zoological laboratory of the University of Oklahoma. Aided by a grant from the Faculty Research Fund of the university and by a grant-in-aid of research from the American Association for the Advancement of Science.

With a group of species so interesting zoologically and at the same time so imperfectly known, it is understandable that false notions should have grown up about the spadefoot toads. The most notable of these is that these animals spend most of their time underground, emerging rarely except after heavy rains, breeding and then returning immediately to burrows again to await another rain. Many have accepted this uncritically, despite the fact that it leaves no obvious manner in which they could secure food.

The source of this idea is in the rarity of the solitary or hermit spadefoot of the East, *Scaphiopus holbrookii holbrookii* (Harlan), which by all accounts behaves very differently from all the other eastern frogs and toads. Ball (1936) in emphasizing the scarcity of authentic records of this species in New England points out that it had not been seen at New Haven, Connecticut, between 1879 and the time of his own studies. Concerning its breeding he adds, "in the North during the past 125 years only about sixteen instances have been recorded, all associated with heavy rains."

As the western prairies and plains became settled during the past century, other species of *Scaphiopus* were described. Almost immediately, the ideas about the rarity of the eastern spadefoot became applied to some of them. As late as 1935, I heard statements clearly implying that the plains spadefoot, *S. bombifrons* Cope, seldom emerges from the ground, and then only once a year to breed. One former Oklahoma biologist (Brooks, 1930) stated his belief that animals of this species found buried in hard-packed soil in western Oklahoma could not have emerged for several years. The finding of spadefoots (also in Oklahoma) imprisoned in balls of clay several feet below the surface under conditions very difficult to explain (Decker, 1930) may also have furthered this belief.

Those who have studied the spadefoots most carefully in their native haunts, however, have nearly always noted

that they are abroad and feeding much more commonly than supposed (see Kellogg, 1932; Campbell, 1933; Ball, 1936; and others) and I have observed that some species are relatively easy to find except in hot, dry weather. I have captured hundreds of individuals of *S. bombifrons* and *S. couchii* on roads at night and have seen the latter feeding upon insects beneath street lights with garden toads of two species. On the other hand, adults of *S. hurterii* Strecker have been found only during and immediately after rains and their juveniles rarely except on moist ground.

The truth seems that some species (*e.g.*, *S. h. holbrookii* and *S. hurterii*) are more difficult to find than others (*e.g.*, *S. bombifrons*, *S. couchii* and *S. hammondii* Baird). Part of this no doubt is the result of a real difference in the habits of the two groups (see beyond) but some of it is due to the fact that the first group tends to dwell among trees, whereas the second prefers open lands. All species, so far as known, feed above ground at night and none of them spend most of their time below the earth's surface under the usual conditions of their respective native habitats. The generalization that spadefoots as a group seldom emerge from underground burrows is, therefore, without foundation in fact.

For seven years, I have studied the habits and distribution of the spadefoot toads in Oklahoma and have made more limited observations in New Mexico (Bragg, 1941c). I have seen hundreds of breeding congresses and have made detailed notes of breeding sites, breeding dates, behavior of the adults while breeding, feeding and moving about, noting the breeding calls of adults and the structure and behavior of tadpoles at all stages. I have watched metamorphosis in several species both in the laboratory and in the field. In many parts of Oklahoma, trips at night during times of breeding have been taken to find out, by following the calls, just what relation there might be between relative numbers of this or that species in one ecological community and another adjoining one.

During the earlier parts of this study I was often accompanied by my friend and former colleague, Dr. Charles Clinton Smith, who has also observed practically everything new recorded here and has greatly aided my understanding of the spadefoots through informal discussions. So closely have Dr. Smith and I worked together that it is quite impossible to separate his observations from my own even if either he or I wished to do so. This paper was originally planned as a joint contribution, but circumstances have intervened which make impossible Dr. Smith's checking my interpretations of our common efforts. For this reason, it has seemed wiser to us both to publish under my name alone and for me to assume complete responsibility for the conclusions drawn.

At the beginning of this study, *S. couchii* was the only spadefoot about which there was no question, taxonomically. *S. hammondii*, *S. intermontanus* and *S. bombifrons* were much confused: *S. multiplicatus* was questionably distinct from *S. hammondii*: *S. h. holbrookii*, *S. h. albus* and *S. hurterii* were similarly confused. Tadpoles of *S. hammondii*, *S. bombifrons*, *S. couchii* and *S. h. holbrookii* had been described, but an unfortunate mishap had confused those of *bombifrons* with those of *hammondii*. At the present time, due to the efforts of several investigators the tadpoles of all except the still questionable *S. h. albus* are known and the general distribution of the species within the genus is fairly well understood. Tadpoles of *S. h. holbrookii* and *S. couchii* were described by Wright (1929); those of *S. bombifrons* by Wright (1929) under the name *hammondii* (see Bragg, 1941); those of *hammondii* by Smith (1934) under the name *bombifrons*; those of *intermontanus* by Tanner (1939); those of *multiplicatus* by Taylor (1942) and those of *hurterii* by Bragg (1943). The general range of each species in the genus was approximately mapped by Tanner (1939) from specimens which he had seen, but recent work indicates some general extensions to be necessary, e.g., Carl's (1942) recently finding *hammondii* in South-

ern British Columbia. Similarly, records of *S. couchii* in western Oklahoma (Bragg, 1941a) and new records published herewith of *S. hurterii* in the Arkansas Valley of southern Osage County, Oklahoma (Fig. 5) place these species farther north than formerly reported.

The breeding behavior of *S. bombifrons* has been reported by Trowbridge and Trowbridge (1937), Bragg (1941c) and Bragg and Smith (1942); something about that of *S. couchii* by Ortenburger (1926); that of *hammondii* by Gilmore (1924) (who also had specimens of *bombifrons* in his collection of tadpoles), Goldsmith (1925) and Bragg (1941b, c); that of *S. h. holbrookii* by several investigators, most recently by Ball (1936); and that of *S. hurterii* in notes by Smith and Leonard (1937) and Bragg (1943). The breeding behavior of *S. h. albus*, *S. intermontanus* and *S. multiplicatus* each still await study by any one favorably situated to observe them.

Because of the rapid advance in the study of the biology of the spadefoots in recent years, it has seemed wise to me, while reporting specifically my own observations in Oklahoma, to include a summary of all our knowledge to date about the natural history and ecological relations of these interesting animals and to attempt a synthesis of this as expressed as a phylogenetic tree. To do so at least has the advantage of focusing attention on problems still left unsolved, even though further observations may change somewhat the conclusions drawn here.

CLASSIFICATION

The genus *Scaphiopus* has eight known forms. Tanner (1939) separated two groups of species into two subgenera, *Spea* and *Scaphiopus*. I follow Tanner in this concept for reasons which appear further on.

Class Amphibia

Order Salientia (Anura)

Family Scaphiopodidae

Genus *Scaphiopus*

Subgenus *Scaphiopus*

S. holbrookii holbrookii (Harlan), 1835.

S. holbrookii albus (Garman), 1877.

S. hurterii Strecker, 1910.

S. couchii Baird, 1854.

Subgenus *Spea*

S. bombifrons Cope, 1863.

S. hammondii Baird, 1859.

S. intermontanus (Cope), 1883.

S. multiplicatus Cope, 1863.

S. bombifrons and *S. hammondii* were long considered conspecific by many and subspecifically related by others. Smith (1934) was the first to demonstrate clearly their specific independence. This was confirmed by Tanner (1939); and I found it easy to distinguish the two on the basis of calls as well as structure of adults and tadpoles (Bragg, 1941c). *S. hurterii* has similarly been suspected to be conspecific with *S. h. holbrookii* or only a subspecies of the latter. But, according to Smith (1937) and confirmed by Tanner (1939), the skulls of the two are so different as to make them specifically distinct. Recently I have had opportunity to study the breeding behavior, metamorphosis and tadpoles of *S. hurterii* (Bragg, 1943) and found that these all differ in detail from those of *S. h. holbrookii* as described by Ball (1936) and others. I therefore concur with Smith and with Tanner in considering these distinct forms. *S. intermontanus* has not commonly been recognized as distinct from *S. hammondii*, which it seems closely to resemble. I have not personally seen this form, but according to Tanner (1939) its skull and other characters, as well as its tadpoles, are different from those of the latter. *S. multiplicatus* of Mexico is little known, but Taylor (1942) has shown its tadpoles to differ materially from those of *hammondii* and concludes that if the tadpoles of the latter have been correctly designated by me (Bragg, 1941b) then *multiplicatus* is specifically distinct from *hammondii*. As stated earlier *S. couchii* has always been recognized specifically, but *S. h. albus* of southern Florida is still a questionable form (Wright and Wright, 1933) although recognized by Stejneger and Barbour (1939).

As now understood, adults and tadpoles within *Scaphiopus* may be separated by use of the following keys.²

A. Adults.

1. Metatarsal tubercle elongate or sickle-shaped; parotid gland present (may be indistinct); size large. (Subgenus *Scaphiopus*) 2
1. Metatarsal tubercle rounded (not sickle-shaped); parotid gland absent (or present and very large in *multiplicatus*); size small. (Subgenus *Spea*) 5
2. Pectoral glands present; parotid and tympanum distinct 3
2. Pectoral glands absent; parotid and tympanum indistinct.
 - Scaphiopus (Scaphiopus) couchii* Baird
 3. Ratio of head length to head width approximately 18/21; back sometimes roughened but not with restricted patch of fine dark spiny tubercles just back of eyes 4
 3. Ratio of head length to head width approximately 22/25; dorsum mostly non-tuberculate except for a characteristic patch of small, dark, short spines immediately behind the eyes.
 - Scaphiopus (Scaphiopus) hurterii* Steereker
 4. Color brown to light green, usually not particularly light-colored.
 - Scaphiopus (Scaphiopus) holbrookii holbrookii* (Harlan)
 4. Color lighter with "great amount of white on back, flanks, and upper surface of limbs; vermiculated irregular white bands."
 5. Interorbital osseous boss present.
 - Scaphiopus (Scaphiopus) holbrookii albus* (Garman)
 5. Interorbital osseous boss absent 6
 6. Frontoparietal fontanelle present 7
 6. Frontoparietal fontanelle absent.
 - Scaphiopus (Spea) intermontanus* Cope
 7. Skin quite tuberculate on back, with several folds; head Bufo-like, short and thick; tibial gland present.
 - Scaphiopus (Spea) multiplicatus* Cope
 7. Skin mostly smooth or only slightly tuberculate; no folds on back; head longer; tibial gland absent.
 - Scaphiopus (Spea) hammondi* Baird

B. Tadpoles

1. Size large; color light to medium grey or brown, never very dark; shape rounded and full-bodied. (Subgenus *Spea*) 2
1. Size small; color very dark grey or very bronzy, sometimes nearly black. (Subgenus *Scaphiopus*) 5
2. Jaws with a prominent beak in upper and corresponding notch in lower; jaw-muscles well developed.
 - Scaphiopus (Spea) hammondi* Baird

² Modified from Tanner (1939) and Bragg (1942c) and extended by use of the data of Taylor (1942) and Ball (1936) on tadpoles and of Cope (1889) on adults of *multiplicatus*.

³ Tadpoles of *S. h. albus*, still unknown.

2. Jaws with no prominent beak and notch; jaw-muscles not overdeveloped 3

3. Anterior of body much more depressed than posterior; appearance from above somewhat angular (Taylor, 1942, pl. 2, Fig. 3). Labial formula 4/4, the 1st upper row very short and across midline.

Scaphiopus (Spea) multiplicatus Cope

3. Anterior of body not much more depressed than posterior; appearance from above rounded; labial formula not 4/4, or if so, then the lowest row of teeth, rather long 4

4. Color alive, coppery; labial formula 2/4, the first upper row long and continuous except for a slight interruption in the middle.

Scaphiopus (Spea) intermontanus Cope

4. Color dark to light grey, never coppery; labial formula 4/4, 3/4 or 5/4, lowermost row of teeth long.

Scaphiopus (Spea) bombifrons Cope

5. Ground color coppery bronze with golden spots or sheens and much iridescence; labial formula 4/4, 2/4, 5/4, 3/6, or 5/5, the 1st two labial rows discontinuous, the last two continuous.

Scaphiopus (Scaphiopus) couchii Baird

5. Ground color dark grey to almost black, no dorsal iridescence or sheen 6

6. Labial formula variable (6/6, 6/5, 5/6, or 5/5), only the first two rows complete.

Scaphiopus (Scaphiopus) holbrookii holbrookii (Harlan)

6. Labial formula 4/5 or 3/4 with some variability dorsally. Only lowest (ventral) labial row typically complete.

Scaphiopus (Scaphiopus) hurterii Strecker

DISTRIBUTION

The home of the spadefoots is in the Southwest. Only *S. holbrookii holbrookii* and *S. h. albus* have spread any great distance eastward. *S. hammondii*, *S. intermontanus* and *S. couchii* are confined to quite xeric habitats in short-grass plains and deserts. *S. bombifrons* occurs here also, but extends eastward in the mixed-grass prairies of southwestern United States. *S. hurterii* is known only from woodlands and mid-xeric savannahs in Texas, Oklahoma and Arkansas.

Because Oklahoma is moist and low in the southeast and high and dry in the west, particularly in the northwest, and because its geographic position is almost central for possible dispersal of spadefoot toads, no area of comparable size exists more suitable for learning the ecological requirements of these animals. Extensive studies

have shown the spadefoot toads here to be quite strictly limited in accordance with the ecological divisions. (For a detailed description and map of the ecological divisions, see Bragg and Smith, 1943; see also Fig. 1).

There are four species in Oklahoma, two (*hammondii* and *bombifrons*) in the subgenus *Spea*; the others (*harterti* and *couchii*) in the subgenus *Scaphiopus*. Figs. 2 to 5 show their county distributions as now known. It is to be especially noted that *hammondii* has been taken only in the northwest, its eastern limit of distribution being in Woods County (Smith, 1934) practically coincid-

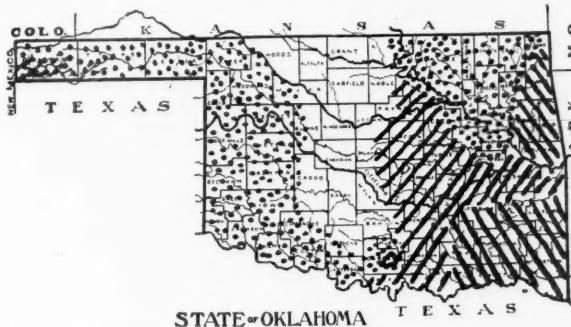


FIG. 1. Generalized ecological map of Oklahoma. Data from Bragg and Smith (1943) q.v. for more detailed map. Stipple=tall-grass prairie in northeast, short-grass plains in west. //////////////////////////////////////////////////////////////////=Oak-hickory savannah. \\\\\\=Oak-hickory-pine woodland. Unmarked=mixed-grass prairie.

ing with the broad ecotone between the short- and mixed-grass prairies.⁴ It is especially interesting, however, that I have failed to find this species in southwestern Oklahoma, although it is here that the short-grass plains extend farthest eastward. On the other hand, *S. couchii* (a species also restricted to short-grass plains in Oklahoma)

⁴ The record of *S. hammondii* Baird in Payne County (Ortenburger, 1927a) is based upon a specimen of *S. bombifrons* Cope. I suspected this on ecological grounds and therefore asked Mr. C. H. Pope, of the Field Museum, to check on the identity of the specimen. His letter, dated November 31, 1941, confirms the identity as *S. bombifrons* Cope. Through the courtesy of Dr. Edw. H. Taylor, I have seen the specimen reported by Smith (1934) as *S. hammondii* from Woods County and confirm the record as of *S. hammondii* Baird.

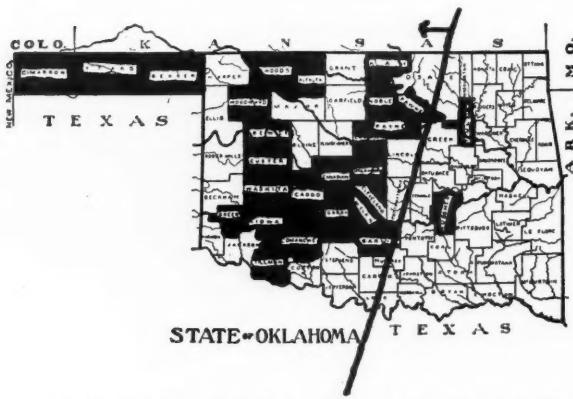


FIG. 2. County distribution of *Scaphiopus bombifrons* Cope in Oklahoma from specimens examined and literature records. The diagonal line indicates the approximate eastern limits of abundance. All records east of this are from limited local populations in prairie-islands in the savannah.

has been found *only* in the southwest, ranging eastward within this ecological community to central Stephens and Jefferson counties in the south, but only to southern Caddo County farther north. Its northern extension within the short-grass plains goes into southern Custer County, but it has not been taken north of this even at the most favorable times. This strongly suggests that *S. couchii* has recently extended its range northward, per-



FIG. 3. County distribution of *Scaphiopus hammondii* Baird in Oklahoma. All records from the literature.

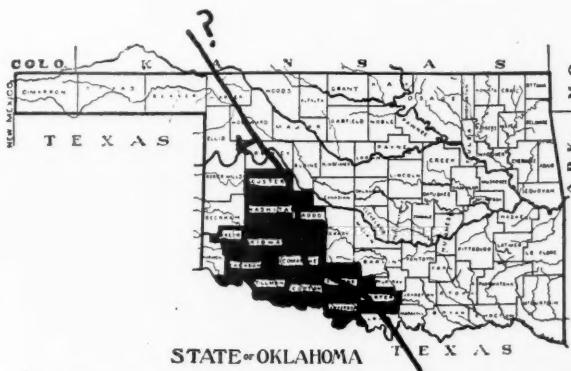


FIG. 4. County distribution of *Scaphiopus couchii* Baird, in Oklahoma. All from specimens personally examined.

haps during the recent dry phase of the climatic cycle which apparently ended with the summer of 1937.

S. bombifrons is the most widely distributed and most abundant of its genus in Oklahoma. It occupies the short-grass plains of the west and south, but is extremely abundant in the mixed-grass prairies of central Oklahoma and is also present east of this in islands of prairie in the woodland-savannah, at least to Hughes and Tulsa counties (Fig. 2). Just as *S. couchii* in western Oklahoma is



FIG. 5. County distribution of *Scaphiopus hurterii* Strecker in Oklahoma ?= record of *S. h. holbrookii* (Harlan) by Ortenburger and Freeman (1930) thought probably to be *S. hurterii* (see text).

distributed much as *Bufo compactilis* Wiegmann (Bragg and Smith, 1943), so *S. bombifrons* is distributed with *Bufo cognatus* Say. So close are these correlations that we are reasonably sure in predicting the presence of either of these spadefoots in any habitat in Oklahoma where the corresponding *Bufo* is found. As with *Bufo cognatus* (Bragg, 1940) *S. bombifrons* is most abundant in higher areas of the grasslands and does not enter woodland proper nor extensive flood plains at all. For example, I stood one night after a heavy and violent rain on the flood plain of the Canadian River in western Cleveland County, listening to the calls of practically all the species of frogs and toads present in the region. Calls of *S. bombifrons* reached me as a continuous roar from the prairies on either side of the river, some from congresses over two miles distant as later determined during the same night. But not a single *S. bombifrons* was seen or heard on the flood-plain, even though all the flood-plain inhabiting species were in chorus from sloughs of several types on the plain. Comparable observations were made on the Cimarron River in Logan County by Dr. Charles C. Smith and by us together on the Washita in Garvin County and by me at various other points on the Canadian and North Canadian rivers through several seasons.

S. hurterii has formerly been reported from Oklahoma only a very few times, usually as *holbrookii* (Smith and Leonard, 1934; Smith, 1937; Bragg, 1940b; 1942a). During 1941 it bred successfully in many places in eastern Oklahoma⁵ and is now known to be quite abundant in all the woodland and savannah areas (Fig. 5). Except in Oklahoma it is known only in western Arkansas (Smith, 1937) and the eastern part of Texas. Comparison of Fig. 1 and Fig. 5 will reveal an apparent inconsistency, for county records are shown on the latter which seem not to

⁵ I am indebted to Dr. A. P. Blair for all records in northeastern Oklahoma here reported. The remainder are from specimens collected myself or sent to the University of Oklahoma Museum of Zoology. For permission to report the latter, I am indebted to Dr. A. I. Ortenburger.

conform to the ecological situation implied by the former. This is because *S. hurterii* tends to follow the flood plains of the larger streams westward where their flood-plain forests interdigitate with the grasslands. They have been found on the Arkansas, Cimarron, Canadian and Red rivers west of their general range as indicated by the line passing through Fig. 5, but just how far westward they extend is uncertain. During the period when this species was commonly considered as *S. h. holbrookii*, Ortenburger and Freeman (1930) reported the latter in the western tip of the panhandle near the Cimarron River. I have not been able to locate the specimens upon which this record is based, but I strongly suspect that they had *S. hurterii* (as also did Smith, 1937). Assuming this to be the case, *S. hurterii* may be expected in any part of Oklahoma along the larger flood-plains, but generally distributed only in the woodland and savannah in the eastern half of the state.

HABITS OF THE SPADEFoot TOADS

As with most animals, the habits of the spadefoot toads center about three major activities: (1) protection, (2) feeding and (3) reproduction. I give below a summary of my observations on these, principally in Oklahoma.

Spadefoots are protected from death from drying by their nocturnal and fossorial habits. All are nocturnal, most of them strictly so, although *S. bombifrons* at all ages in captivity may quickly come to the surface during daylight and may feed if it should rain or if the ground be sprinkled liberally. I have kept a number of them for more than a year in a large box to observe their reactions and have seen them hopping about in this in cool, moist, spring weather. I have never succeeded in finding them active in nature in the daytime, however, except while they were breeding, and then only a few times. During midsummer the animals in the box could seldom be induced to emerge from the soil, even by a liberal wetting with a garden hose.

To determine the relative resistance to drying, I placed twelve adult *S. bombifrons* with a comparable number of each of three species of Oklahoma *Bufo* (*B. cognatus*, *B. w. woodhousii* and *B. americanus americanus*) in a large box of moist sand indoors where they lived for several weeks. (It is to be remembered that *B. cognatus* is much like *S. bombifrons* in its ecological requirements, that *B. a. americanus* is a woodland and savannah form in Oklahoma, and that *B. w. woodhousii* occurs in nature to some extent in habitats occupied by each of the others.) All these emerged regularly at night to feed upon beetles which I placed in the box; and all behaved normally. Then I allowed the moisture gradually to evaporate in the dry air of the laboratory. Within three days of the time when the surface of the sand appeared to be thoroughly dry, no *Scaphiopus*, no *B. a. americanus* and only a few *B. cognatus* emerged at night, although most of the *B. w. woodhousii* continued to come up regularly. As the sand became drier, none appeared above the surface and after three weeks, when I judged that most of the moisture had disappeared, I dug into the sand. All the animals were found at the extreme bottom of the box. All the *B. a. americanus* and all but two *Scaphiopus* had died, and these two were thin and weak. Two of the smaller *B. cognatus* and one *B. w. woodhousii* were also dead. From this it would seem that *S. bombifrons* is less tolerant than the garden toads of its natural habitat to lack of moisture and more comparable to the toad of the woodlands and savannahs.

In a larger box kept out of doors, there were seventeen adult *S. bombifrons* with forty-four juvenile *B. cognatus* and one adult *S. couchii*. The spadefoots had lived here through two summers and winters, feeding upon insects attracted by a light placed above the box. Occasionally, the earth was dug away carefully to determine the nature of the underground burrows made by the animals. There was nothing distinctive about those made by any of them. The animals simply backed into the earth as far as they

were inclined to go and remained there. When the earth was moist, all merely covered themselves, some of the garden toads even remaining with their heads protruding throughout the day. Whenever it became drier and the air hotter, all dug more deeply and emerged less frequently to feed, in extremely hot dry weather in mid-summer not emerging at all. At all times there was a clear positive correlation between the tendency to dig down (and also how deeply the animals dug) and the dryness of the air and soil. There was also a correlation between the placement of the burrows and objects available near or under which they could be formed. When the ground was bare, most specimens burrowed around the edges of the box and only a few nearer its center. During three summers, when the box was left undisturbed for several weeks, plants sprouted and grew in the soil. Under these conditions about half of the burrows were close under the plants and all but two or three of the remainder still near the sides of the box. I could find no difference between *S. bombifrons* and *B. cognatus* in these things, except that *B. cognatus* emerged under drier conditions in the daytime than *S. bombifrons*.

Correlating these experimental findings with field observations, one can conclude that (1) both of these prairie species tend to be nocturnal, the spadefoot more so than the toad; (2) both form burrows the depth of which is correlated with lack of moisture; (3) both tend to emerge quickly after rain (or artificial wetting simulating a storm), the toad more quickly than the spadefoot; and (4) both tend to bore into the earth beside objects (usually plants) where (a) the ground may be softer, (b) it is more shady, and (c) the burrows are not easily observed.

Field observations indicate that there is an interspecific difference in some of these matters among the spadefoots. *S. couchii* has been found out feeding in large numbers when it was much too dry to expect *S. bombifrons*. On the other hand, *S. hurterii* has rarely been seen except during and after rain. Juveniles of this species

have been found a few times feeding along dry roads on cool nights in spring (May) and autumn (October) and one very young *S. hurterii* (not more than a month from metamorphosis) was taken along a moist, shaded run in the daytime, in June. This, incidentally, is the only specimen of any spadefoot toad which I have ever found active in nature in daylight, except in breeding congresses, and except at and immediately after metamorphosis.

Virtually nothing is known about the predators molesting *Scaphiopus* and I have learned nothing during this study. Many *S. bombifrons* and *S. couchii* and some *S. hurterii* are killed during moist weather by cars on roads, especially near pools during breeding activities. *S. bombifrons* has been noted to have a sticky, musty-smelling, mucoid secretion of the skin, often exuded in some amount when the animal is handled. Whether or not this is protective, I do not know.

The feeding habits of adult spadefoot toads are closely comparable to those of the garden toads, as I have observed through several years of study of both. I have never known either to attack a vertebrate although I have had very tiny toads (*Bufo*) and young of *Scaphiopus*, *Rana* and hylids with adults of *Scaphiopus bombifrons*, *S. hammondii* and *S. couchii* and with garden toads on many occasions. Individuals of all these species, as well as of *S. hurterii*, are very adept at catching arthropods and they seem to have little discrimination (except for size) among types of insects and spiders. I have seen adults of *S. bombifrons* capture flies, hymenopterans, moths of several families (Saturniidae, Noctuidae, Notoodontidae and others), beetles (Carabidae, Cincindellidae, Chrysomellidae and Scarabaeidae), bugs of several kinds, including pentatomids, and miscellaneous spiders. Young juveniles of *S. bombifrons* and *S. hurterii* feed readily upon many kinds of small insects and arachnids (Trowbridge and Trowbridge, 1937; Bragg, 1941, 1943), although the former seems to learn some food selection by trial and error.

The food of spadefoot tadpoles is of special interest. Most kinds of North American tadpoles are said to be primarily vegetable eaters, although it is well known that those of most garden toads and of the frogs do eat dead animal matter, including dead specimens of their own kind, as well as small animals taken incidentally with algae or plant debris. In contrast, many kinds of spadefoot tadpoles tend to be carnivorous and some of them show marked cannibalistic tendencies. If a piece of liver be placed in a dish containing large tadpoles of *S. bombifrons* or *S. hammondii* the animals attack it fiercely, shaking it violently (for all the world like a puppy with a slipper) and chewing out pieces to swallow. Similarly, if the smaller tadpoles of *Bufo* are placed with those of *S. bombifrons* they disappear rapidly. If one *Scaphiopus* tadpole becomes injured, the others immediately attack it, tear it to pieces and, with *S. hammondii* at least, and perhaps also *S. h. holbrookii* (Ball, 1936), they sometimes do not wait for an injury before the attack. Tadpoles of *S. hurterii* and *S. couchii* also will eat meat, but I find no record of cannibalism in these species. It should be carefully noted, however, that Trowbridge and Trowbridge (1937) found that a completely meat diet was not adequate for normal development of *S. bombifrons* and I have confirmed it for this species as well as observing it consistently in all other Oklahoma species, both in pools and in laboratory cultures.

(To be concluded)

NATURAL SELECTION AND THE BIRTH-RATE¹

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WITH regard to his theory of natural selection, Darwin said "the expression often used by Herbert Spencer of 'the survival of the fittest' is more accurate, and is sometimes equally convenient." Had Darwin's foresight been equal to his understanding, he would have professed conversely that Spencer's expression is more convenient and is sometimes equally accurate, for to-day "the survival of the fittest" is a household term used to denote no more than the personal survival of those individuals most fit to endure in the struggle for existence, a definition inadequate for natural selection. More comprehensive but also incomplete as a definition of natural selection is the interpretation of "the survival of the fittest" to be the tendency for the racial survival of those inheritable factors that promote personal survival. Natural selection, however, is not only the personal survival of those fittest to survive, nor is it only the racial preservation of those genetic factors that promote personal survival. Also subject to the selective process are the inheritable factors that affect the reproductive proclivity of the organism, and that, solely as such, are causally unconnected with the traits of the individual influencing its personal survival. For instance, the prolificacy that characterizes the parasitic existence—a single human tapeworm, *Taenia saginata*, producing as many as one billion fertilized eggs during its lifetime—is a cumulative result of the selective process that, while possessing positive survival value, does not promote the viability of the individual, *i.e.*, it does not increase the individual's chance of survival.

¹ Contribution from the Chesapeake Biological Laboratory, Solomons, Md.

Genetic factors increasing the rate of birth tend to be perpetuated by natural selection for the same reason that hereditary factors favoring personal viability are likely to be preserved, namely, that the variants they characterize are more prone to leave descendants (likewise bearing these factors) than are the not-so-modified competing types. However, the racial survival of a genetic factor, whether a determinant of personal survival or a determinant of reproductive capacity, is dependent upon the combined effectiveness of the fertility and the viability of the genetic type it characterizes. For example, a genetic factor conducive to personal viability may fail to be perpetuated if it causes an inadequate reproductive rate, or is genetically linked with factors detrimental to the fertility of its carriers. The vigor of plant and animal hybrids which is frequently unperpetuated because of concomitant sterility serves as an illustration. Similarly, inheritable factors that increase the birth-rate may not have positive survival value if they occasion a lessening of the individual's chance of survival. As an illustration, factors increasing the production of eggs beyond the ability of the parental birds to hatch and feed their progeny generally have not been perpetuated by natural selection, since they result in a retributory reduction in the viability of the offspring.

In a like manner, inheritable modifications unfavorable to the personal survival of the individuals in which they occur may have a selective advantage, if they induce a compensatory rise in the birth-rate or are genetically linked with factors that augment the rate of natality. The relatively high fertility of the feeble-minded, and some of the sexual behaviors of the lower animals, *e.g.*, mating scents, calls and colorations, which, while lessening the chance of their personal survival, increase the frequency of their cohabitation, are exemplifications. Similarly, genetic modifications that lower the rate of reproduction may be preserved, if they are associated with a compensatory gain in the individual's chance of

survival. The evolution of internal embryonic development and the evolution of the intellectual faculties comprise such modifications. While they have diminished the prolificacy, these evolutionary developments have conferred a compensatory increase in the viability of the progeny (culminating in man, whose lifetime fertility is of the sparingly low value of less than three births per parental pair in the United States, but of whose offspring the strikingly high ratio of approximately 80 per cent. survive until the end of their reproductive span).

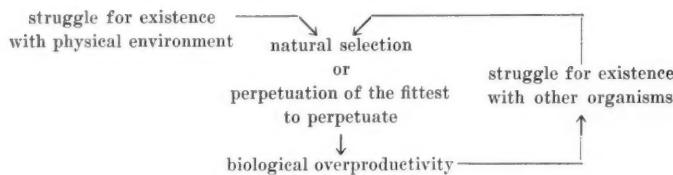
The racial survival of genetic factors that affect the birth-rate and the racial survival of genetic factors that affect personal survival are dependent upon both the fertility and the viability of the genetic types these factors characterize. Perhaps better than by Spencer's phrase with its existing ambiguity, natural selection may be defined as "the perpetuation of the fittest to perpetuate," which connotes the fitness of the individual for reproduction as well as for personal survival, and also the tendency for the perpetuation of genetic factors that impart either or both of these qualities to the individual.

Because of its overcrowding, resulting from its greater productivity, a variant with a fertility-favoring mutation eventually suffers a loss of viability, *i.e.*, it suffers a decrease in the individual's chance of survival. On the other hand, a variant with a viability-favoring mutation, *per se*, need not later undergo a loss of fertility. Instead, as its population pressure mounts, its viability more likely will be reduced to that of its not-so-modified ancestor. Since fertility-favoring mutations generally lower the individual's chance of survival, while viability-favoring mutations, *per se*, do not reduce the fertility, there is a tendency for natural selection to result in an increasing birth-rate and a consequently decreasing viability.

The perpetuation of viability-favoring modifications that are directly associated with a reduction of fertility, however, has caused the reproductive rate to undergo decreases in some lines of evolutionary development.

Such are the modifications that increase the vitality of the eggs, embryos or young at the expense of the number produced, *e.g.*, an increased supply of yolk and internal embryonic development. More generally, however, natural selection results in a growing birth-rate, and, because of the increasing overproductivity, a consequently diminishing viability. This has given rise to a fertility in many organisms that is of a magnitude disproportionate to the environmental adequacies and that results in a superabundance of offspring. For example, the lifetime fertility of the big tree, *Sequoia gigantea*, is a figure that would tax the imagination, yet in a stationary population an average of only one of the millions of seeds produced by a single individual survives to the age of the parent. Such fertility results in an enormous and a generally useless mortality of pre-adult stages. Nevertheless, an otherwise superfluous rate of reproduction may be entirely useful to some species during repopulation, following the decimation caused by seasonal or fortuitous environmental changes or following dissemination to a new environment.

Darwin deduced, from the principle formulated by Malthus (1803)—“the constant tendency in all animated life to increase beyond the nourishment prepared for it,”—that this biological overproductivity is the cause of the struggle for existence and thus of natural selection (Darwin, 1859). As has been previously indicated to the converse, however, the process of natural selection, which has increased the fertility beyond the environmental adequacies, is the cause of biological overproductivity. While the interorganismal competition, which results from biological overproductivity, constitutes a part of the struggle for existence, the physical conditions of the earth engender a struggle for existence with the physical environment and impose a directly selective action upon each new variation before it meets with organismal rivalry. As is indicated in the following diagram, biological overproductivity is the result, and only secondarily a causal factor, of natural selection.



In opposition to the occurrence of mutations, which constantly augments the variety of hereditary characters, natural selection tends to decrease the variability within a species. In addition to natural selection, there is another process that tends to decrease genetic diversity, which consists of the loss to the race of genetic factors through the process of segregation. In sexual reproduction, one member of each pair of genes possessed by either parent is ordinarily lost to each offspring because of the segregation of homologous genes in the reduction division. Due to such random loss, newly acquired mutations, whether beneficial or unfavorable, may not become established in the race, and established genes, even though they possess a survival advantage, may be reduced in frequency to the point where they are eliminated (Dobzhansky, 1941).

The chance of loss of parental alleles to the mature filial generation and hence to the species is generally independent of the birth-rate of the species, since, while the chance of loss of parental factors to the filial generation at birth is diminished by a greater fertility, the individual offspring's chance of maturation is usually commensurately decreased by a greater rate of reproduction. However, if the genetic factor confers a very large selective advantage, there may be less chance of its loss to the mature filial generation and to the species the greater the birth-rate of the species. With a higher rate of reproduction, more offspring will receive the favorable allele, and hence, if its selective advantage is sufficiently great, a larger number of favorably modified offspring will survive to maturity.

As representatives of the opposite extremes of reproductive capacity, man and the oyster can be used to illustrate the effect of the size of the birth-rate on the loss of such favorable mutations through segregation. A female human is unlikely to produce more than thirty offspring in a lifetime, and, at the prevailing rate of reproduction, would actually produce fewer than three. There is a sizable chance that a favorable mutation not present homozygously in both human parents would be lost to the race, regardless of its selective advantage, because of its failure to appear in any of the comparatively small number of offspring produced. A single female oyster, *Ostrea virginica*, on the other hand, is capable of producing several hundred million progeny. The chance of loss to the race of a beneficial parental gene because of its failure to appear in such a large filial generation at birth is insignificant. While it is inconceivable that a single mutation, or any combination of genetic factors, would confer a selective advantage enabling all the favorably modified oyster offspring to survive to maturity, it is probable that certain genes would confer a selective advantage great enough to enable the production of considerably more than three adult progeny per parental pair, which is the limit of man's reproductive ability at his prevailing rate of reproduction. If the genetic factor confers a sufficiently large selective advantage, the chance of its loss through segregation will vary inversely with the reproductive rate of the species.

Generally speaking, the later in ontogeny such favorable genetic modifications exert their selective advantage, the greater will be the chance of their loss to the adult population. The later the mutation is expressed, the smaller is the number of progeny to which it was transmitted that are still surviving at the time it confers its selective advantage, and the less is the chance that any of the favorably modified offspring will survive to maturity.

Since the perpetuation of a race is dependent upon its

fertility as well as upon its viability, species with a continually declining fertility are eventually eliminated from the evolutionary procession. The subsiding birth-rate of man apparently is due to a growing hesitancy to procreate, coupled with an extending knowledge of contraceptive methods (Pearl, 1939), but, whatever the cause, a continued decrement of his rate of reproduction will result in his eventual extinction. Until man's realization of the relationship between copulation and procreation, it is unlikely that the prenatal desire for offspring possessed survival value, and consequently was not subjected to the selective process. During this period, natural selection freely intensified man's urge for personal survival, an urge that later became deterrent to his desire to bear offspring. With his eventual realization of the copulation-reproduction relationship, the inherited instincts of self-preservation became manifested in his intentional repression of procreation, a procedure that has its origin in prehistoric times (Carr-Saunders, 1922).

Although the discommodiousness of children has always existed and, except for interims such as the current war, is in general diminishing, apparently, during the last half century, man's subjective evaluation of his necessities, as reflected by his attenuating birth-rate, has been outgaining his increasing provisions. This is presumably an intensified manifestation of the survival urge, produced by relatively recent cultural changes.

The modern distending acquaintance with the methods of birth control is also a major cause of man's attenuating rate of birth, and, when this knowledge has reached a saturation point, it will not of itself cause a further contraction of his rate of reproduction. Further decline of the human birth-rate will then depend upon a continuing disproportionate increase of man's subjective standard of living. Since this has negative survival value, and since, with man's improving viability, his fertility is increasingly subjected to the selective process, it is likely that the natural selection of fertility-favoring factors

eventually will become manifested in a gradually expanding rate of birth. It is presumed that the increasing birth-rate will be controlled for the welfare of humanity, and not regulated solely by the demands of the individual or for the ambition of the nation.

Inheritable factors that elevate the rate of reproduction and that, unless causing a correspondingly large reduction in the viability of their possessors, have been and will be further preserved and intensified through the processes of mutation and natural selection, may be placed in biological, psychological and sociological categories. The biological factors may be subdivided into those that augment the number of offspring in a single birth and into those that amplify the frequency of birth. Multiple ovulation, multiple development of a single zygote, and other inheritable factors conducive to multiple birth comprise the first category. Among the biological characters that amplify the frequency of birth are a prolonged period of viability of gametes; an extended reproductive span, spreading in both directions and involving fitness for survival until loss of reproductive ability; less prenatal mortality and maternal mortality of childbirth; and other improvements in the structural and functional processes of reproduction.

The two major psychological factors increasing the frequency of birth, which if inheritable have been subject to intensification by natural selection, are the desire for sexual intercourse, lending an evolutionary support to Freudian psychology; and the prenatal desire for children, dating from the time of man's realization of the connection between copulation and reproduction. Prospective sociological changes amplifying the frequency of birth, our social heritage also being subject to the selective process, are an increasing social security, social encouragement of young marriages and large families, and disapprobation of the single and childless states.

Because of the expanding usage of birth-control measures, the subjection of the desire for sexual intercourse

to the action of natural selection is diminishing. This is also true of several of the biological factors that affect the birth-rate. By the same token, the sociological factors affecting the rate of reproduction and the psychological factor of the desire for children are becoming increasingly disposed to the selective process.

The recent birth-rate spurt in the United States was presumably a manifestation of the desire for children that had been provoked by impending war-engendered circumstances, *i.e.*, sexual isolation and unnatural death. When these war-born conditions transpired, they made it impossible for many to reproduce, and resulted in a resumed declination of the reproductory rate in the United States. After the Global War, the human birth-rate will continue its general decline unless and until the aforementioned social changes become effective in reducing the application of birth-control measures.

RECAPITULATION

(1) Natural selection may be defined as the perpetuation of the fittest to perpetuate, which connotes the perpetuation of genetic factors that increase fitness for reproduction as well as of those that increase fitness for personal survival.

(2) Because of the overcrowding resulting from fertility-favoring mutations, such mutations generally lead to a reduction in the viability, *i.e.*, the individual's chance of survival, of the modified types. While viability-favoring mutations that directly reduce the fertility have occurred in some lines of evolutionary development, viability increases, *per se*, do not usually result in a lowering of the fertility. Thus, there is a tendency for natural selection to result in a growing birth-rate and a consequently decreasing viability.

(3) Natural selection is the direct cause, and only secondarily a result, of biological overproductivity.

(4) Chance of loss of very favorable genetic factors through segregation varies inversely with the repro-

ductory rate of the species and directly with the extent of individual development at the time the selective advantage of the factor is expressed.

(5) Man's diminishing birth-rate is due to a spreading knowledge of contraceptive methods, coupled with a growing hesitancy to procreate, the latter being a recently intensified manifestation of the urge for personal survival, an urge that was excessively enlarged by natural selection before the prenatal desire for children became subjected to the selective process.

(6) Since the expression of man's survival urge in the renigement of reproduction has negative survival value, intensification by natural selection of inheritable biological, psychological and particularly sociological characters that increase the birth-rate should eventually result in an increasing rate of reproduction.

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THE NATURALIST IN AMERICA IN 1942 ± 75 YEARS^{1,2}

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IN those regions of the western hemisphere that had developed a high degree of autochthonous civilization, such as those of the Nahuas and Mayas of Mexico and the Incas of Peru, for example, a knowledge of nature had developed very fully before the arrival of the Europeans, and, looking back at our continental past, it is there that we should be able to find the first American naturalists.

Although traces of the knowledge of nature in the original cultures have remained for us in their monuments, and although a few final sparks could still be seen during the first few years of European domination, as, for example, in the magnificent herbal organized in 1552 by the Indians, Martin de la Cruz and Juan Badiano, nevertheless, one can say that on the whole the intellectual development of the primitive Americans in those regions in which they reached a high level was interrupted abruptly with the introduction of European culture.

In 1570, there arrived in New Spain the eminent Francisco Hernandez, private physician to Philip II, who sent him to study the plants and animals of the colony, and who Reed (1942) assumes "was probably the first botanical expedition sent out by a government." With Hernandez, who was afterwards called "the Pliny of New Spain," there began on our continent four centuries ago the era of naturalists of European orientation.

¹ This paper was prepared for the annual meeting of the American Society of Naturalists, which was scheduled to be held in New York City on December 29, 1942, but was cancelled owing to war conditions.

² The writer feels very much indebted to Dr. José Zozaya, for criticism of the manuscript, and to Dr. and Mrs. William Vogt, also for critical reading of the manuscript, as well as for translating to English the Spanish original.

Slowly, along with the advance of European colonization, the study of nature progressed, but it is not really until the eighteenth century that we can speak of "American naturalists," in the United States as well as in the rest of the countries of this continent.

In the United States, as Kofoid says, there was "an indigenous biology springing from the soil, field and forests and assisted in part by the dependence of medicine upon biology. The biologists of the American tradition were naturalists interested in the flora and fauna of the New World. The names of Catesby, Audubon, Bachman, Halbrook, Bartram, Rafinesque, Say, Isaac Lea and many others adorn the pages of biological history in the earlier years."

In Mexico, at about the same time, there were the Spaniards, Sessé and Cervantes, and the Mexicans, Alzate and Mociño, together with Bustamante and others, who started the Mexican school of natural history that, as Kofoid observed in the United States, was by preference concerned with the study of plants and animals with a marked interest in the medical applications of these studies. Especially was this true in the field of botany, in which the Mexican school was heir to the extensive Aztec knowledge of medicinal plants. The initiation of these studies followed a similar path in the rest of the hemisphere, at about the same time, as we can see in the work of Mutis in Colombia, Molina in Chile, Azara and Muniz in Argentina, etc. One must not forget, however, the profound influence on American science exercised by that illustrious traveler, Alexander von Humboldt.

We can say then, as might be logically expected, the first inspiration of the students of our hemisphere was the knowledge of the animals, plants and minerals that existed in it. And this state of things was the one that still prevailed up to seventy-five years ago, up to the last third of the nineteenth century.

These last seventy-five years have seen, all over the world, a profound change in the point of view of the men

dedicated to the investigation of nature. With the consistent use of the microscope, begun in its modern form about the middle of the eighteenth century, with the perfection of physics and chemistry that offered their apparatus and reagents to facilitate the study of living creatures, the biological laboratory was born, with the character that it has had during the last hundred years, and thanks to whose work the life sciences have progressed to a remarkable degree.

Unfortunately, in certain sectors there arose also an unjustified conflict between those scientists who followed the old methods of natural history in its classical form, especially in the field and in the museums, and those who were taking the new trails of experimentation.

The veteran North American zoologist, L. J. Cole (1941), sums up this situation in a graceful article reviving youthful memories:

Where our graduate group worked there was an iron grill which separated the museum from the zoological laboratories. It separated almost as effectually the "species splinters" from the "sperm chasers." . . . The field naturalist and museum worker felt that the "closet zoologist," as he dubbed the laboratory investigator, was working under such artificial conditions that its findings had little relation to animals in "natural" surroundings. Above all, that he had little conception of taxonomic problems, and the chances were that if he should meet in the wild the animal on whose tissues he was working he would not recognize it. The embryologist, physiologist or cytologist on his part accused the taxonomist of playing a game about on a par with arranging a collection of postage stamps, and of splitting genera into species, and species into subspecies, merely for the doubtful distinction of getting his name attached to the specimens and embalmed for posterity and for eternity along with them.

These conflicting points of view became so accentuated in later years that with the great success of the experimental laboratory sciences the rest of the departments of natural sciences were to a certain extent neglected.

Such an attitude, world wide, was undoubtedly one-sided, and very soon voices were raised in warning against the danger that was being run in abandoning the classical methods of natural history, not only because of their own objective value, but also because of their close

relationship with the experimental work of the laboratory to which their findings offer a great deal in the way of points of departure for other investigations.

Twenty years ago, in 1923, Professor Ashworth in his address as president of the Section of Zoology of the British Association for the Advancement of Science, commenting on what he felt to be the state of the animal sciences then, said:

The danger that morphology will be pushed to excess is long past; the peril seems to me to be rather in the opposite direction, *i.e.*, that some of our students before passing on to research receive too little of that training and discipline in exact morphology by which alone they can be brought to appreciate how the components of the living organism are related to one another and to those of allied species or genera, and how they afford, with proper handling, many data for the evolutionist. I plead, therefore, for the retention of a sound and adequate basis of morphology in our zoological courses. . . . Another of the basal supports of our science an appreciation of which or better still a training in some branch of which we must encourage is the systematic or taxonomic aspect. The student or graduate who is proceeding to specialize in experimental zoology or genetics particularly requires a sound appreciation of the fact that the accurate determination of the genus and species under investigation is a primary requisite for all critical work, it is part of the fundamental data of the experiment and is essential, if for nothing else, to permit subsequent observers to repeat and perhaps to extend any given series of observations.

The situation pointed out in England in 1923 appeared to be the same in the United States even in 1938, when Professor F. R. Lillie, referring to the future of the zoological sciences wrote:

There is a strong tendency among zoologists at the present time, especially those devoted to experimental methods, to believe that these subjects (taxonomy, comparative anatomy, paleontology, embryology and geographic distribution) have played their main role already in the development of zoology; and so in many places these fields of zoological education are neglected. The consequent failure, where such a situation exists, to appreciate the richness and interrelationships of animal life, the perfection of adaptations and the immensity of time in the geological ages that have gone into their creation is a grave defect in the education of the zoologists. . . . The basic descriptive disciplines of zoology are, moreover, live subjects for research. The background is occupied by the descriptive and systematic observational disciplines, which need and continue to receive constant attention, if only in the service of experimental investigators which require increasingly exact observational bases.

And this interesting opinion of Lillie's, even more interesting coming from an individual so well versed in and acquainted with laboratory techniques and methods, is the same that Crocker expresses, referring to the future of botany, in an article published the same year, 1938:

Finally, the conditions met in a laboratory are limited and principles established in the laboratory need to be tested and modified as to limitations and breadth of significance by tests under the more varied conditions in the field and in nature.

In the above quotations we have tried to make evident a point of view with respect to the modern orientation of the natural sciences that appears to be universal, since Ashworth and many other scientists in Europe have expressed the same opinions as have Lillie, Crocker and many more in America.

However, since the aim of this paper is to concern itself especially with the role played by the naturalists of our continent, it may be well to state something that in our opinion explains the prejudice that has been noted in the natural sciences of America, to some extent, against field and museum studies.

We said at the beginning of this paper that with the arrival of the European conquerors and colonizers in the sixteenth and seventeenth centuries, the aboriginal civilization of America among those people who had succeeded in developing any, was abruptly cut off and replaced by that imported from Europe, especially from England, France, Spain and Portugal, nations that played the preponderant part in the formation of the present American countries, and that besides were centers of European culture of that time.

Now in Europe the methodical study of flora and fauna had already been initiated by the Greek and Roman scientists—Aristotle, Theophrastus, Pliny and many others; later, during the long period of the Middle Ages, new contributions, although in small numbers, were being made in these fields. And about the dawn of the Renaiss-

sance and during its prime, especially under the influence of men such as Ray, Linnaeus, Tournefort, Gesner, Aldobrandi and many others, there arose a veritable furor for the systematic knowledge of the flora and fauna of little Europe, a knowledge that by the beginning of the eighteenth century was well under way. Each country could rely on acceptable catalogues of its plants and animals more or less correctly classified.

So that when with the beginnings of the nineteenth century the biological laboratory got its vigorous start, thanks to the patient early work of the naturalists, European students already had the indispensable morphological and systematic base from which to take off for their new experimental explorations.

In America the situation was different. With the aboriginal culture interrupted, and the European culture transplanted here during the sixteenth and seventeenth centuries, we received Europe's scientific knowledge in its current state, it is true, but we did not receive nor could we have received the preliminary work of centuries during which it had become established.

On a continent many times larger than Europe were implanted the advanced methods of the biologists, in their many aspects, without there having been previously fulfilled the basic and fundamental requirement of a systematic classification of the fauna and flora.

It is very interesting to note that Kofoid, in the article to which we referred before, speaks of the influence that French thought exercised in the United States, especially through Franklin, Jefferson and Agassiz, who was a disciple of Cuvier; of the influence of German thought through the many young Americans who went to round out their studies in the famous laboratories of Leuckart, Boveri and many others; and of the English influence, particularly with the coming of Huxley to Johns Hopkins, as well as through Osler and others. Now these were the currents that vitalized and succeeded in establishing on the brilliant foundation on which later we have seen it

develop, the experimental and laboratory work of modern North American biological science. But Kofoid speaks also of the naturalists in the American tradition interested in the flora and fauna of the New World. It was precisely the Catesbys, the Audubons, the Rafinesques and their kind who, for the most part unconnected with universities or official institutions, felt least the influence of European thought, and in consequence began their work following the biological path that had been traversed centuries before by their colleagues of the Old World, and that even up to to-day, in all the Western Hemisphere with its immense area, and most especially in the Latin American countries, we have only just started on.

Consequently the conditions created in Europe by the flowering of experimental and laboratory work, although extremely fertile, had however as a lamentable corollary, a certain neglect of the classic basic disciplines of natural history—a neglect which on our continent has been even more acute, not only because of the greater extent of our territory and the consequent richness and variety of our flora and fauna, many times greater than Europe's, but also, and perhaps more important, because we did not have the advantage of the work of earlier generations of naturalists who in Europe were collecting and classifying plants and animals during a period in which European civilization did not even exist in the New World, or had barely achieved a foothold through the bloody struggle of the conquest, and the precarious events of colonial days.

The present struggle in which our countries are engaged has demonstrated how little we know of the natural history of our continent. When it has been necessary to send soldiers into strategic zones, at times practically unexplored and uninhabited, vital and urgent questions have arisen: What animals and plants are found there? Which are useful and which might be injurious? What do we know of their biology that might orient us in their

utilization and control? Occasionally information can be found in libraries and museums to clear up these mysteries; frequently no information at all can be obtained and it is necessary to begin research at once, regretting that at the proper time sufficient emphasis was not laid on this kind of investigation, that some people, perhaps, might have considered "antiquated."

The war has pointed up also, with unusual emphasis, the vital value of nature conservation in all its phases. And this work requires unavoidably a previous knowledge and an adequate description and classification of the resources to be conserved.

In our opinion, the classic work of the naturalist in the basic descriptive disciplines still holds an indisputable place in the study of nature throughout the world "... if only in the service of experimental investigators which requiere increasingly exact observational bases," as Lillie says.

But on the American continent the demand is even more urgent for a larger number of naturalists to study its seas, investigate its rivers and explore its jungles and mountains. The catalogue of our plants and animals has hardly been started, and it is vitally necessary that it be completed not only for the benefit of those scientific investigators that would discover its endless finds to be a great interest in clearing up different biological problems, but also from the point of view of its practical use.

In fact, many American countries whose diet is deficient can find through the systematic exploration of their flora and fauna new sources of food to improve the popular diet.

Besides, progress in communications, with the daily use of the automobile and airplane, represents a potential danger in the transportation of disease vectors, whose distribution can only be known adequately after exploring all corners of the hemisphere.

Because of the emphasis that we have laid on the basic disciplines of the natural sciences, which, in our point of

view, have been quite unjustly forgotten, it might be thought that we underestimate the experimental work of the laboratory, since we have said nothing in its defense. Nothing is further from our thoughts. If we do not raise our voice in favor of the laboratory, it is because we feel that it needs no defense, since what the experimental studies have done in the past for the advancement of the natural sciences is so well known and so justly esteemed, as well as are the great things that may be expected of them in the future.

Since by preference we have been occupied personally in laboratory work, we could not advise the abandonment or neglect of such study; on the contrary, we know its value and believe that it should be furthered as much as possible. Nor are we considering a return to the Linnaean era, which, in the present state of the natural sciences, would result in sterility. But we do believe that it is necessary to preserve a due respect for the field work and museum work of the "naturalist" *sensu strictu*.

The growth and progress of science have always been cumulative and cooperative. Each investigator who honestly tries to wrest one of her secrets from nature, whatever the end he pursues or the methods he employs, makes a useful contribution. The contribution may be of such character that its theoretical importance or its practical applications are immediately apparent, and no one will deny its value. At other times the data obtained, for a thousand extrinsic or intrinsic reasons, appear to be without any importance, condemned beforehand to oblivion. However, if the result was arrived at honestly and is consequently reliable, however small it may appear it will be an element that later will enter into the construction of larger theoretical concepts or will be useful in achieving some practical end.

There is no need, therefore, in our opinion, to try to evaluate in hierachial form that which each branch of the natural sciences can contribute to the total knowledge of nature, and to the control, direction and utilization of

nature for the benefit of man—an end that has always been the goal towards which the masses of humanity have moved since the moment, lost in the darkness of time, in which our most remote ancestors began to know, and later to organize their knowledge of those things mineral, vegetable and animal that might profit them, or, on the contrary, that might harm them.

From an abstract point of view, all the branches of the natural sciences are equally useful as techniques for knowing nature. In isolation, it is possible that not one of them may be considered complete or perfect. Together, they complement each other; each one makes its own contribution, that, linked with that of all others, will make possible the building up of an overall picture of nature.

In our opinion, then, one of the most important aspirations for the next seventy-five years is that of achieving a harmonious understanding among the different branches of the natural sciences, in such a manner that, each one working in its own special field, with its own resources, can contribute its partial findings, which, united with the rest, will serve to construct the whole that will enable us to better interpret nature.

One must not forget that if each one of the branches of the natural sciences has its peculiar problems and uses special techniques to solve them, all together they have in common the use of one basic tool—the scientific method, which, based on observation and experiment, and eliminating in consequence the prejudices and personal caprices of the investigator, governs equally the work of the morphologist and systematist as that of the physiologist and geneticist. And in all cases, if it is correctly employed it should give results comparable in biological significance, no matter what the special techniques by which they have been obtained.

Another goal to be reached in America is the achievement of better understanding among the naturalists of the whole continent, from Alaska and Canada to Argen-

tina and Chile. In the past each one of our countries has felt a closer bond with one or more of the European countries than with its neighbors of the western hemisphere. It is still common to meet naturalists in the Latin American countries who, although well acquainted with European science, especially that of France, are practically ignorant of what the United States has done in this field, believing that in that country the spirit of the business man, the industrialist, in one word, the promoter, leaves no room for the development of scientific thought. On the other hand, not a few scientists of the United States are equally ignorant of what their colleagues south of the Rio Grande are accomplishing, and they think that in the republics of Latin origin the arts, poetry and literature, mixed with politics, are the only pursuits of the inhabitants, incapable of the rigorous work of scientific investigation.

For an American science of biology to be developed that shall be really productive and worthy of respect, we must end such a state of things. Fortunately, the necessities of the moment that to a certain extent have obliged our continent to be self-contained culturally, and that have forced thousands of scholars to explore it in all directions, are forming bonds of friendship and fellowship among the naturalists of the twenty-two Americas, who, knowing each other, are beginning to esteem each other.

The Latin American naturalist is becoming convinced that the great development of science in the United States has much to offer him, and he no longer persists in believing that all cultural inspiration must come from Europe. The Anglo-Saxon naturalists, on their part, have had an opportunity to see with their own eyes what is being accomplished, if on a more modest scale, in the Latin American countries, and with such contact with their colleagues of another language, there has been born a genuine appreciation for the work that many of them are pursuing.

Besides, and this is very important, both have become

aware that in the field of natural science in its broadest meaning there exists such infinite problems of such magnitude that one country alone could never solve them satisfactorily, and as a consequence they may never be solved definitively unless every nation offers its contribution to their solutions.

With all their mistakes and limitations, the contribution of the last seventy-five years of the natural sciences on the American continent is something to be proud of. If the next seventy-five years succeed in giving their just due to each of the different branches of the biological disciplines, without distinction or preference for any one of them, much will be accomplished.

And if an effective scientific union can be achieved, a real sincere, disinterested and honest cooperation among all the naturalists of the hemisphere, from Hudson Bay to the Strait of Magellan, we can not only feel proud of the accomplishment, but we shall be able to say then that there is an American science of biology.

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REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

IN these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of *THE AMERICAN NATURALIST*, in that they deal with the factors of organic evolution. *REVIEWS AND COMMENTS* are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California. All opinions are those of the reviewer.

The Haplolepididae, a New Family of Late Carboniferous Bony Fishes. A Study in Taxonomy and Evolution. By T. STANLEY WESTOLL. *Bull. Am. Mus. Nat. Hist.*, 83, 1944: 1-122, pls. 1-10, figs. 1-52. \$1.75.

THIS new family is erected for one of the many phyletic lines into which the primitive actinopterygian or paleoniscoid fishes are now supposed to have evolved. The Haplolepididae were very small fishes, with large scales, greatly reduced opercular bones, few fin rays that were but slightly or not at all branched, and certain features trending toward the holostean type. The paucity of meristic parts and general structural reductions may have been related to dwarfing.

These fossils are brought so nearly into life by Westoll that they all but swim across the page. They are skillfully interpreted as having been surface-inhabiting fishes of warm marshy waters that were deficient in oxygen. Indeed I see in the restorations remarkable likenesses to the viviparous topminnows, the Poeciliidae, of similar Recent waters. The resemblances include a terminal mouth, a flattish back, a small posterior dorsal fin, and a caudal region so oriented as to remain in the water as the fish swims against the surface film. Of particular import is the occurrence in both groups, and in certain other surface-swimming teleosts, of lateral line organs on the ventral surface. Ventral lateral lines in the Actinopterygii are therefore not confined, as the author suggested, to the Haplolepididae. Since they occur in such teleosts as the Poeciliidae and certain Atherinidae, their

occurrence in the Carboniferous family may not have been an archaic feature.

General remarks are included on the phylogeny of the Actinopterygii, the main line of fishes. The transition from the sharklike chondrostean type through the "Sub-Holosteis" and the supposedly polyphyletic Holosteis to the Teleostei, involving particularly the change from a strongly heterocercal to a homocercal caudal fin, is correlated with the adoption of a marine habitat by the fishes which had previously lived in quiet fresh-waters. The modification in fin structure is related to the increased density of the environment, the lesser need of an upward driving mechanism and "the loss of the structural devices for providing 'lift'". I regard this interpretation as erroneous for the following reasons: living fishes with ordinary heterocercal tails are bottom dwellers, and nearly all are marine; motions of a heterocercal caudal would seem to produce a downward rather than an upward thrust; the adjustment in specific gravity could more readily have been made by a reduction in the air bladder. I would look on the transformation in caudal structure rather as an adaptation to provide the increased speed called for in the open waters of the newly invaded seas. Parallel changes are suggested by the pseudo-homocercal caudal of the speedy surface-swimming lamnid sharks and of the fossil genus *Cladoselache*.

Plant Viruses and Virus Diseases. Second revised edition. By F. C. BAWDEN. Waltham, Mass.: Chronica Botanica Co.; New York: G. E. Stechert and Co., 1943: i-xi, 1-294, figs. 1-48. \$4.75.

THE first edition of this book was published at Leiden, Holland, in 1939. Due to the Nazi invasion the plates were lost and the book was out of print within a year.

Until less than a decade ago, work on the viruses had been largely in the hands of bacteriologists and pathologists. Fortunately, the attention of chemists, physicists, entomologists, serologists and other specialists has been turned toward solving some of the perplexing problems

of this branch of science. An inevitable result is that the publications are widely scattered in apparently unrelated journals, and in language unfamiliar to many biologists. The author of this text deals primarily with the nature of viruses themselves, and only in a general way with the diseases caused by such agents. In spite of the war, research in this field has continued to make rapid progress, thereby justifying the thorough revision and extension which is presented in the current edition. Under present difficulties the writer has succeeded admirably in bringing together the new knowledge of this field.

Chapter I surveys the general problem and includes a definition of a virus, a history of virus diseases and a review of the problem of nomenclature. The symptomatology of plant virus diseases is well covered in the next two chapters. The transmission of viruses and their relationship to insect vectors, both of which are important problems of long standing, are brought up to date in the fourth and fifth chapters. In the next chapter "virus strains, mutations, and acquired immunity" are given due consideration. The similarity and differences between immunity in plants and in animals are clearly presented, together with a thorough coverage of the botanical phenomena involved. The Serological Reactions of Plant Viruses, a subject of interest because of its bearing on the current problem of classification, is the topic of chapter VII.

Chapter VIII deals with the "purification of viruses." In the following chapter the chemical and physical properties of the purified virus preparations are considered. In the tenth chapter the author presents, in terms a biologist can comprehend, the highly technical subject of "optical properties of the purified virus preparations." Chapter XI takes up the "inactivation of viruses," a subject of importance in the description and identification of viruses. The physiology of the host plant in relation to the virus, the controversial subject of classification and the technics of disease control are discussed in chapters

XIII to XV. The need of a system of classification based upon the virus is emphasized. The writer points out the necessity of a knowledge of the virus, its host relations and methods of transmission, if sound control measures are to be devised. General control measures are briefly discussed.

In a final chapter the origin and multiplication of viruses are considered. The controversy of whether viruses are living or non-living may be unimportant, but it has aroused much interest and is well presented in these final pages. With the questions of origin, multiplication and the living versus non-living nature of viruses, the author leaves his reader to carry on.

The biologist who has not been able to follow the voluminous literature in this field should find Bawden's book a very welcome addition to his library. It gives a clear, concise, excellently illustrated discussion of most of the literature, by one who has been actively engaged in the study of the chemistry and physics of viruses. The book is beyond a doubt a significant contribution to our scientific literature.

J. ARTHUR HERRICK

NOTICES OF NEW BOOKS AND ARTICLES

The Living Mosaic. By CARL EPLING. Faculty Research Lectures, University of California, Los Angeles. Berkeley and Los Angeles: University of California Press, 1944: 1-26, figs. 1-16. \$0.25.—The modern field of speciation is very interestingly presented in this lecture, by a skilful combination of generalizations and examples. Species are treated as one of the highest levels of biological organization. The interaction of heredity and variation is stressed. Geographical variation and segregation are clarified by a brief epitome of Epling's thorough studies on the pitcher sage, *Lepechinia*. Isolating mechanisms are then given emphasis, with illustrations of the types of mechanisms taken from the author's studies of sages, *Salvia*. Inferences on the past history of evolutionary lines from biogeographical data, are exemplified from Epling's recently published study of *Drosophila pseudo-obscura*.

The Ecotype. By J. W. GREGOR. *Biological Reviews*, 19, 1944: 20-30.—Ecotypic differentiation is defined as an hereditary change occasioned by the selective action of the habitat. Such speciation may be independent in respect to different environmental trends, and may be regional or strictly local. It is most frequent in species with wide latitudinal or altitudinal distributions. Clines correlated with gradual changes in climate comprise a limited number of distinct populations. Zones of intergraduation are usually narrow. Effects of hybridization may spread without destroying the integrity of the hybridizing forms. "Ecoclinal subspecies," with objectively delimited ranges, should be recognized nomenclaturally on the subspecies level, but "eco-clinal ecotypes," with subjectively delimited ranges of ecotypic variation, are not to be accorded subspecies names.

The Distribution of the Salamanders of the Genus *Plethodon* in Eastern United States and Canada. By ARNOLD B. GROBMAN. *Ann. N. Y. Acad. Sci.*, 45, 1944: 261-316, figs. 1-11. \$0.75.—Much of interest to students of speciation is included in this paper. Emphasis is placed on geographical equivalence, though the new term "syngeographs" for geographical equivalent or sympatric forms hardly seems needed. The terms sympatric and allopatric are also used, and it is properly pointed out that there was no warrant in my suggestion (*Am. Nat.*, 77, 1943: 174) that these terms are etymologic hybrids and should be replaced by "compatrie" and "alipatrie." It is demonstrated that the ranges of the salamanders treated are closely correlated with areas of forest types, with the extent of continental glaciation and with physiographic provinces. The ranges of these animals are apparently limited by recognizable barriers. Terminal raciation is finely illustrated.

Guide to Higher Aquarium Animals. By EDWARD T. BOARDMAN. *Bull. Cranbrook Inst. Sci.*, 21, 1944: 1-108, 60 figs. \$2.00.—In characteristically attractive style the Cranbrook Institute of Science presents another of its guides to nature. It is skillfully written down and should serve effectively in introducing the local fishes, amphibians, and aquatic reptiles that can be cared for in aquaria to the youngsters of Michigan and adjacent regions, and to older folks who would stay young by cultivating a personal acquaintance with these fascinating animals.

A Review of the Halfbeaks or Hemiramphidae of the Philippines and Adjacent Waters. By ALBERT W. C. T. HERRE. Stanford Univ. Publ. (Univ. Ser.; Biol. Sci.) 9: 39-86, 1 map. \$1.00.—A general account of the characteristics and natural history of this highly specialized family of synentognathous fishes precedes the revision. Most of the species belong to the viviparous genera *Zenarchopterus* and *Dermogenys*, the classification of which is largely based on the secondary sexual modifications of the fin rays in the males.

Entomology for Introductory Courses. By ROBERT MATHESON. Ithaca, New York: Comstock Publishing Co., 1944: i-xiv, 1-600, frontisp., figs. 1-500. \$5.50.—Another fine book on insects comes from Cornell, the home of entomology in America. After connecting the insects, through their near relatives, with other animals, the author gives an account of insect anatomy adequate for the taxonomic study that follows, order by order. The systematic section covers more than half the pages but not so large a proportion as in some other recent texts. Families are distinguished in a series of previously tested keys. Interesting statements are included on the life histories and economic relations of important insects. Illustrations abound. The four final chapters deal in an elementary way with "Insects in Relation to Human Welfare." Glossary, Bibliography, and Index close the attractive volume.

Manual of Human Protozoa. By RICHARD R. KUDO. Springfield, Illinois: Charles C Thomas, 1944: i-ix, 1-125, figs. 1-29. \$2.00.—This new book adds another volume to the already ample number of publications devoted to aiding the student or medical man interested in war diseases caused by protozoan parasites. The printing and illustrations are of the usual high order of the Thomas publications. There are, however, many mistakes of sentence construction, such as misplaced adverbs and the dropping of articles, that cause confusion in the reader's mind. Several instances of questionable descriptions of morphology are noted. The author follows the usual method of calling the parasite a commensal whenever there is any doubt regarding its pathogenicity. The directions for making permanent preparations of protozoa in fecal samples needs to be radically revised, as it is doubtful whether a student would be successful in his efforts

when following these directions. Since it is confined to the important human parasites the manual will be of value to medical and pre-medical students.—A. E. WOODHEAD.

Gestation Periods: A Table and Bibliography. Compiled by J. H. KENNETH. Imperial Bureau of Animal Breeding and Genetics. Edinburgh: Oliver and Boyd, Ltd., 1943: 1-23. 2s. (orders and payments to be made to Imperial Agricultural Bureaux, Central Sales Branch, Agricultural Research Building, Penglais, Aberystwyth, England).—The data apply to mammals only, and are arranged alphabetically by English vernaculars. Average, minimum, or maximum figures are presented (all when available), with references to the 341 items in the bibliography. No appraisal of the data is offered, except for the marking by an asterisk of figures based on single cases.

Macquarie Island Its Geography and Geology. By DOUGLAS MAWSON, based mainly on the records of LESLIE RUSSEL MAWSON. Australian Antarctic Expedition 1911-14, Sci. Repts., (A) 5, 1943: 1-194, pls. 1-37, maps and figs. 1-46. 1£, 15s.— Though primarily a geological and geographic study, this report contains an account of the fauna and flora of Macquarie Island, in the Antarctic south of New Zealand, along with statements on the extinction of the fur-seals and of the ground parakeet and on the precarious status on the island of the penguins and sea-elephants. It is held to be the duty of civilization to set up here a preserve to save the interesting fauna and flora from extinction. Macquarie Island is the sole breeding ground for birds and mammals that forage over a vaste expanse of sea.

AMERICAN SOCIETY OF NATURALISTS

The American Society of Naturalists met in Cleveland on September 12-14, under the presidency of Dr. FAY-COOPER COLE. The Symposium on Biology and Human Progress was attended by about 150 persons. The program was as follows:

1. Biology and the Public Mind, Charles V. Taylor, Stanford University
2. Plants and the Material Basis of Civilization, Edmund W. Sinnott, Yale University
3. The Rehabilitation of Biological Research and Education in War Stricken Countries, Robert Chambers, New York University

There were elected to membership in the society: J. B. BUCK, University of Rochester; GEO. L. CROSS, University of Oklahoma;

MAX DELBRUCK, University of Tennessee; BORIS EPHRUSSI, Johns Hopkins University; KATHERINE ESAU, University of California at Davis; G. L. GRAHAM, Rockefeller Institute; IVAN JOHNSTON, Harvard University; D. H. LINDER, Harvard University; PHILIP A. MUNZ, Pomona College; GREGORY PINCUS, Clark University; ALBERT TYLER, California Institute of Technology; FRANZ VERDOORN, editor *Chronica Botanica*. As Honorary Members to fill vacancies there were elected: G. H. PARKER, Harvard University; R. G. HARRISON, Yale University; F. R. LILLIE, University of Chicago; all have served as President of the Society and all joined it before 1900.

As officers of the Society there were elected, as President, E. W. SINNOTT, Yale University, as Vice-President, K. S. LASHLEY, Harvard University, and as Treasurer, T. M. SONNEBORN, Indiana University. To fill three vacancies on the editorial board of THE AMERICAN NATURALIST caused by retirement under the by-law establishing the editorial board, there were elected J. H. BODINE, University of Iowa, P. W. WHITING, University of Pennsylvania, and SEWALL WRIGHT, University of Chicago.

Following the annual dinner of the society which was attended by 61 persons, the Presidential address was delivered by FAY-COOPER COLE of the University of Chicago, on "Some Problems of Human Racial Development and Migration."

WILLIAM RANDOLPH TAYLOR, Secretary

AMERICAN SOCIETY OF GENETICISTS

Secretary LAWRENCE H. SNYDER writes that there is no news to report, since the meeting of the American Society of Geneticists which was scheduled to be held at Cleveland along with the American Association for the Advancement of Science was cancelled at the urgent request of the Office of Defense Transportation.

Other affiliated societies, strong in the conviction that science is an essential element of modern civilization, did meet at Cleveland. There was fair attendance and more than usual interest was displayed, particularly in the discussions of the papers that were read.

SHORTER ARTICLES AND DISCUSSION

CRYPTIC BOBBED ALLELES IN *DROSOPHILA MELANOGASTER*

IN a short note Spencer¹ reported the following features discovered in *Drosophila hydei*. A wild population contained a complete series of multiple alleles at the bb-locus ranging from homozygous wild type to homozygous lethal alleles; the first were discovered by compound effects. The phenotype included such features as bristle length, abnormal abdominal sclerites and some other characters like viability and fertility. The different alleles could act more strongly on one or the other character differentially. There was no complete dominance. Most tested females carried two different bb-alleles.

In a series of experiments on spontaneous mutation in *Drosophila melanogaster* of which a report is now in press, facts were found which parallel more or less those indicated by Spencer for *D. hydei*:

(1) In a set of one-pair cultures from a series of our experimental stocks occasionally flies were found with etched abdomen but completely normal bristles. The insufficient chitinization of the lateral edges of the abdominal tergites (etching) is one of the usual phenotypical effects of the higher bobbed alleles and is found together with the bb-type of bristles. It turned out that the etched flies contained a bb-allele which in homozygous condition does not influence the bristles but produces etching (in a varying percentage of females). Thus among the offspring of 20 pairs of the stock pointed = svr^{pol}, etched females were found in 8 cases in the following proportions: 1 in 43, 15 in 71, 5 in 72, and 5 times most females were etched. These flies were tested with two bb stocks kindly provided by Professor Curt Stern: a low one y g bb with only a small bristle effect, and a higher one called bb-lethal carried as CLB/w^e bbl with a higher bristle effect and also producing an etching effect. The compound effects (as well as localization experiments) demonstrated that the etching in the tested flies was due to a bb-allele with no effect upon the bristles but an effect upon the abdomen. In order to save space the description of the phenotypes of these and other compounds is tabulated below (Table 1).

¹ W. P. Spencer, *Genetics*, 23: 170, 1938.

(2) The same allele was found to be present more or less frequently in other stocks derived by mutation from an original stock called pxbl, but it also was found in a stock svr^{pol}h of completely different origin.

(3) A similar bb-allele was found to be present in a homozygous or heterozygous condition in almost all individuals of a standard a px sp stock (bb^apx sp). Again bristles are completely normal, but a slight tendency toward etching is present. But the compound of bb^{pol} and bb^apx sp, both without a bristle effect, is slightly bobbed and the etching effect is increased. The same is

TABLE 1
AVERAGE PHENOTYPE OF SOME bb-ALLELES AND COMPOUNDS AT 25°
BUT NOT ISOGENIC

bb-allele		Origin		Known modifiers	Bristles phenotype	Abdomen
X ¹	X ²	X ¹	X ²			
bb	bb	y g bb	y g bb		± bb1	± achi 1
+	bb ¹	CIB	w ^e bb ¹	probably present	+, some bb ³ 2-3	± achi 1 achi 3-4
bb	bb ¹	y g bb	"		+	+
bb	bb	y g bb	y g bb	modif. bran	modif. bran	± achi 1
bb ¹	+	w ^e bb ¹	diff. stocks	modif. bran	+	± achi 1
bb ^{pol}	bb ^{pol}	diff. stocks	diff. stocks		+	± achi 1
bb ^{pol}	bb ^{pol}	svr ^{pol} dish	y g bb		1-2	± achi 2
bb ^{pol}	bb ^{pol}	svr ^{pol}	svr ^{pol} eq	modif. bran	2-3	achi 2
bb	bb ^{pol}	y g bb	svr ^{pol} eq		"	1-2
bb ^{pol}	bb ¹	svr ^{pol} dish	w ^e bb ¹		2-3	achi 2
bb ^a px sp	bb ^a px sp	a px sp	a px sp		+	± achi 1
"	"	"	"		± 1	± achi 1
"	bb	"	y g bb		1-2 (2)	± achi 2 (1-3)
"	bb ¹	"	w ^e bb ¹		2-4 (4)	achi 3-4 (4)
"	bb ^{pol}	"	svr ^{pol}		1 (2)	achi 1-2
bb ^{pol} h1	bb ^{pol} h1	diff.	stocks		lethal	lethal
"	bb	"	y g bb		4-5 (2-4)	achi 5 (3-5)
"	bb ¹	"	w ^e bb ¹		5	5
bb ^{pol} h1	bb ^{pol}	svr ^{pol}	svr ^{pol} dish		4-5	4-5
"	bb ^a px sp	svr ^{pol}	a px sp		3-4	3-4
"	"	svr ^{pol} dish	a px sp		5	5
bb ^a px sp h	bb ^a px sp h	a px sp	a px sp		lethal	lethal
bb ^a px sp h	bb ^a px sp h	a px sp	a px sp		4-5	3-4

Legend: classes bb 1-5 = little, 1, 2, 3, complete, shortening of bristles. Classes achi 1-5 = little, more etching, large patches of larval chitin, more larval than imaginal chitin, almost no imaginal chitin. + achi 1 = most flies normal, a few achi 1. ± bb = mostly normal, few beginning bb. Classes in parenthesis: different experiments

true for the compounds bb/bb^{pol} and bb/bb^apx sp, while the bb-test (from y g bb) produces only a very small visible effect in homozygous condition. (See the table where the effects are separated into classes.) A still higher class of effect is produced in the compound with bbl which shows bb^apx sp to be a higher allele than bb^{pol}. Thus the bristle effect has a threshold nearer to normality than the threshold for the abdominal effect, as seen in the behavior of the lowest alleles. But in the higher grades both effects increase roughly parallel with a certain amount of variation. The increase of both effects in the compounds of two alleles both with

subthreshold or almost subthreshold effects in the homozygote is remarkable.

(4) The abdominal effect actually consists of the persistence of larval chitin. In the lower grades this appears only at the edges of the tergites; in the most extreme grades practically no imaginal chitin is formed and the unsegmented-looking abdomen is covered with white, wrinkled larval chitin. All degrees exist between these two conditions (classes 1-5). We will call this the achi effect (from achitinous). In the *a* *px* *sp* stock occasionally a high achi bobbed fly is found, and once even an extreme member of class 5 appeared. This is based upon a higher allele with considerable effect upon both bristles and chitinization, the allele $bb^a\text{px sp}^h$. It is dominant, homozygous almost lethal, and it considerably reduces viability and fertility in compounds so that segregating classes are too small. Flies of grade 5 can be bred only in mass culture. Males with this high allele have a tendency to possess slight deficiencies in chitinization in the genital segments (er. 10% ♂♂) while the bristles remain normal. The compound between the two *a* *px* *sp* alleles is extreme bobbed. If the hemizygous males are viable the cross $bb^a\text{px sp}/bb^a\text{px sp}^h \times bb^a\text{px sp}^h/Y$ produces offspring of which one half are lethal ♀♀ and half are like the mother. Thus a high-grade achi line can be bred as if it were homozygous if the proper males are selected. The number of ♀♀ is small since one half are lethal and the other half poorly viable. There is reason to assume that the high allele arises frequently by mutation in the stock (see below).

Also from *svr^{pol}* which contained the *bb^{pol}* allele a high allele was derived which is a little lower than *bb^apx sp^h* but also homozygous lethal. This allele *bb^{pol}hi* was derived from different stocks of *svr*-alleles, especially from those called *svr^{pol}sd* and *svr^{pol}dish*. In this case its origin by repeated mutation could be proved as the allele appeared repeatedly in selection experiments that were closely watched.

(5) In addition it was frequently observed that in crosses involving *bb*, *bb^{pol}* and *bb^apx sp* a few high bobbed achi individuals appeared among the segregating \pm low bobbed achi or even normal individuals. Tests always revealed the presence of a heterozygous higher *bb*-allele which could have arisen by mutation, which seems to occur much more frequently at the *bb* locus than at any other known locus. It is as a rule discovered only when a compound effect produces the high phenotype.

(6) The test of all these alleles in different compounds reveals that their order is: bb (Stern's $y\ g\ bb$)— bb^{pol} — $bb^{a\ px\ sp}$ — $bb^{pol\ hi}$, bbl (from Stern)— $bb^{a\ px\ sp\ h}$. There is no reason to assume that the bb and achi effects, and also viability and fertility, do not act in a parallel way, though there are threshold differences which put the achi effect frequently about one class ahead of the bobbed effect, while viability and fertility are only affected in the highest classes of those effects. An exact evaluation is rather difficult because the effects are highly modifiable, both genetically and environmentally. Thus it was found that an arc allele (called bran) increases the effect while the a px deficiency, which itself has a similar phenotype to that of bobbed, does not increase the effect. The Dichete inversion is a powerful plus modifier. Quantitative work, using isogenic stocks, is much hampered by the fact that so many stocks contain invisible alleles of bb which become visible in the experiments. Thus the Cy-inversion stock used for such experiments was found to contain such an allele. Another difficulty which affects the reliability of classification comes from the existence of modifiers for the achi pattern. Thus in the presence of the mutant $svr^{pol\ dish}$ the achi pattern loses its irregularity and follows a definite rule: in the higher grades the imaginal chitin is restricted to the central posterior edges of the tergites. (According to old descriptions the mutant abnormal abdomen, near the left end of the first chromosome, which is no longer available, had this phenotype. It was ascertained by localization experiments that this mutant is not involved in our case.)

(7) At the time of the discovery of bb it was found (see Morgan and Bridges 1916)² that hereditary bobbed males appeared occasionally, and this was interpreted as a mutation of the $+\text{bb}$ locus in the Y-chromosome. We observed the same phenomenon repeatedly in bb^{pol} , $bb^{a\ px\ sp\ h}$. The responsibility of the Y-chromosome was easily ascertained in F_1 , F_2 , etc., of crosses of bb -males to attached-X females in which the abnormal Y-chromosomes from the bb -♂ is present in males of even generations but not present in males of odd generations with the expected results upon the phenotype of bb males. But it seems that the most obvious explanation based on a mutation in the Y-chromosome did not suffice because cases were found in which bb -achi males could not contain an X with bb , if the records were correct. But no final solution was found. (The bb -males are greatly enhanced by Dichete which

² T. H. Morgan and C. B. Bridges, Carnegie Inst. Washington, Publ. 237.

produces a huge achi effect of the dorsal type described above.) Another remarkable fact, which does not agree so well with the idea of a mutation in the Y-chromosome is that males with bbl in the X plus the changed Y are normal. More work on these bb males in isogenic stocks, with sufficiently marked X-chromosomes and the use of broken Y-chromosomes is needed, as well as work with isogenic stocks of the different alleles described, comparable to the recent work of Stern³ on ci-alleles.

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VARIATIONS IN THE OFFSPRING OF TETRAPLOID OENOTHERAS

IT is well known that the offspring of the tetraploid *gigas* mutation from *Oenothera Lamarckiana* show wide variability in leaf-width, but the nature of this variation has never been analyzed. *Gigas* mutations have appeared in several other species of *Oenothera*, including *O. grandifolia* described from Eastern Nova Scotia.¹ A single tetraploid of this species appeared in 1936 in the Regent's Park cultures and flowered so late that there was little chance of crossing with other forms. A culture of 35 plants was grown in 1938 from seeds of an unprotected flower. Two plants had larger rosettes than the rest. They grew into larger, taller plants and were recognized as probably triploids. They were subsequently shown² to have 21 chromosomes, mostly in short chains of two or three at diakinesis.

The remainder of the culture were like other *gigas* strains,

TABLE 1

Plant number	Chromosomes	Petal-length	Midleaf ³	Stem height	Per cent. good pollen
inches					
II. 5	28	24-26 mm	15 cm x 41 mm	50	46
II. 2	29	19 mm	10.5 cm x 28 mm	27	16
III. 1	29	19 cm x 42 mm	28	19
III. 5	27	19 mm	13 cm x 47 mm (waved)	39	41
II. 4	27	uprooted	31	15
II. 6	22	24 x 22 mm	15 cm x 21 mm	24	12
II. 8	21	16 x 13 mm	12 cm x 28 mm		

³ *Genetics*, 28: 441-475, 1943; *Proc. Nat. Acad. Wash.*, 29: 351-367, 1943.

¹ R. R. Gates, *Phil. Trans. Roy. Soc. B*, 226: 239-355, 1936, 73 figs.

² G. N. Pathak, Studies in the Cytology of *Oenothera*, *Am. Jour. Bot.* 27: 117-121, 1940, 24 figs.

³ This means a leaf taken half-way up the stem.

strongly biennial, and the rosettes showed wide variation in width of the leaves on different plants. Only 25 survived the winter and flowered in 1939. Material from seven of these plants was collected for cytological study. Their main features are shown in Table 1.

The wide range of variation in leaf-width in *O. Lamarckiana gigas* was formerly described and illustrated.⁴ A *gigas lata* muta-



FIG. 1. Pollen diakinesis in *Oenothera grandifolia gigas*, plant with 29 chromosomes.

tion presumably had 29 chromosomes, the extra one being the same as in *O. lata* with 15 chromosomes. Another derivative of *gigas* with 27 chromosomes^{4a} differed in having smaller leaves and

⁴ R. R. Gates, "The Mutation Factor in Evolution," p. 118, figs. 43-53, 1915.

^{4a} Gates 1915, p. 217.

flowers and 23 per cent. of triangular pollen grains (those of *gigas* being normally quadrangular). Another plant in the same culture, with apparently 27 chromosomes, had very narrow leaves and was highly pollen-sterile.

The variability of the *O. grandifolia gigas* culture was such that it was not always possible to determine by inspection which plants had aberrant chromosome numbers. No. II. 5 was chosen as typical because of its flower-size, leaf-width and height. Its 28 chromosomes were in chains of two or three at diakinesis, with many single ones. Nos. II. 2 and III. 1 had 29 chromosomes which

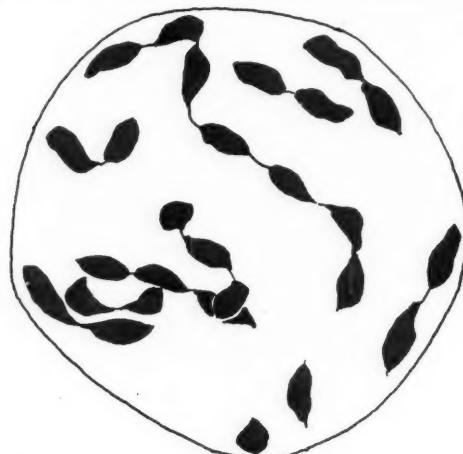


FIG. 2. Pollen diakinesis in *Oenothera grandifolia gigas*, plant with 27 chromosomes.

were nearly all single at diakinesis in some nuclei and in chains up to 4 or 6 in others (Fig. 1). These hypertetraploid plants had smaller flowers and shorter stems than the normal tetraploids and a much higher percentage of bad pollen. They were by no means identical, however, as shown by the foliage. As appears in Table 1, one had much larger and wider leaves than the other. In a larger culture a whole series of $(4n + 1)$ plants would be expected, but on present knowledge they can not be distinguished by their phenotypic characters from $(4n - 1)$ mutants.

Plants III. 5 and II. 4 had 27 chromosomes, mostly in chains containing up to 7 chromosomes (Fig. 2). From Table 1, it will be seen that III. 5 had flowers of the same size as $(4n + 1)$ plants,

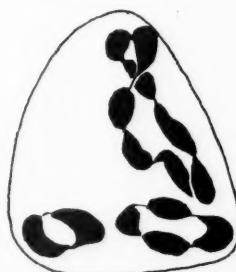


FIG. 3. *O. biformiflora* \times *O. blandina*. Diakinesis showing $8 + 4 + 1_L$ chromosomes.

but a taller stem and a much higher percentage of good pollen. Its leaves, however, were relatively short and extremely broad. A series of $(4n - 1)$ plants may be expected, differing in leaf-width and other characters according to which chromosome is missing.

In addition to the two annual triploids already mentioned, two biennial plants in this culture (see Table 1) had respectively 22 and 21 chromosomes. The latter had narrow, the former very narrow leaves. Even as rosettes they were conspicuously distinct. They also differed markedly in flower-size and in height, the plant with the extra chromosome being larger in both respects.

The wide variability of the various strains of tetraploid *Oenothera* is thus largely accounted for by the occurrence of, (a) offspring with $(4n + 1)$ and $(4n - 1)$ chromosomes, arising through non-disjunction; (b) offspring with $3n$ or $(3n + 1)$ chromosomes. There are also (c) *gigas nanella* mutations in some strains, and (d) occasional diploids, probably of parthenogenetic origin. A complete analysis of these various phenotypes would require cultures of *gigas* on a large scale, and these are difficult to obtain, partly because of the small number of seeds produced per flower. It is clear, however, that the phenotype of these *gigas* variants depends on the particular assembly of chromosomes in each.



FIG. 4. *O. Victorini parviflora* \times *O. blandina*. Diakinesis showing $4 + 4 + 1_L$ chromosomes.

Davis⁵ has recently concluded that *gigas* mutations probably arise usually from somatic chromosome doubling in the fertilized egg, as one of us⁶ originally assumed, but that they may rarely arise from a triploid through the union of two diploid gametes.

In the genus *Oenothera* the most conspicuous changes occurring in hyper- and hypotetraploid forms are in leaf-width, with others in size of flowers, height of stem and the proportion of good pollen. That this is not necessarily the case in other genera is shown by a $4n$ strain of *Antirrhinum majus*.⁷ In this species the hyper- and hypotetraploid plants (descended from a tetraploid produced by colchicine) varied most markedly in the form and color of the zygomorphic flowers. There were also habit differences, but these are not described. The extremes in chromosome number among 274 plants ran, however, from $(4n + 3)$ to $(4n - 5)$.

Three new *Oenothera* catenations may be appended to this note. *O. biformiflora* (broad) \times *blandina* has eight + four + 1_{II} (Fig. 3) *O. Victorini parviflora* \times *blandina* has four + four + four + 1_{II} (Fig. 4) and *O. sackvillensis* Gates has a ring of fourteen. This work was suspended by the war.

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⁵ B. M. Davis, *Genetics*, 28: 269-285, 1943.

⁶ R. R. Gates, *Arch. f. Zellforsch.*, 3: 525-552, 1919.

⁷ J. Straub, *Ber. deut. bot. Gesells.*, 59: 110-113, pl. 1, 1941.

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